THE ANATOMICAL AND FUNCTIONAL CORRELATES OF CATEGORY-SPECIFICITY

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The dramatic effects of brain damage can provide some of the most interesting insights into the nature of normal cognitive performance. In recent years a number of neuropsychological studies have reported a particular form of cognitive impairment where patients have problems recognising objects from one category but remain able to recognise those from others. The most frequent 'category-specific' pattern is an impairment identifying living things, compared to nonliving things The reverse pattern of dissociation, i.e., an impairment recognising and naming nonliving things relative to living things, has been reported albeit much less frequently

The objective of the work carried out in this thesis was to investigate the organising principles and anatomical correlates of stored knowledge for categories of living and nonliving things. Three complementary cognitive neuropsychological research techniques were employed to assess how, and where, this knowledge is represented in the brain: (i) studies of normal (neurologically intact) subjects, (ii) case-studies of neurologically impaired patients with selective deficits in object recognition, and (iii) studies of the anatomical correlates of stored knowledge for living and nonliving things in the brain using magnetoencephalography (MEG).

The main empirical findings showed that semantic knowledge about living and nonliving things is principally encoded in terms of sensory and functional features, respectively. In two case-study chapters evidence was found supporting the view that category-specific impairments can arise from damage to a pre-semantic system, rather than the assumption often made that the system involved must be semantic. In the MEG study, rather than finding evidence for the involvement of specific brain areas for different object categories, it appeared that, when subjects named and categorised living and nonliving things, a non-differentiated neural system was involved.

Keywords: Living and Nonliving things, Object Recognition, MEG, Semantic knowledge, Visual Agnosia.

This thesis is dedicated to my parents, Michael and Veronica Thomas

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CHAPTER 1
INTRODUCTION

1.1 OBJECTIVE

The objective of this thesis was to investigate the structure, organising principles and anatomical correlates of stored knowledge for categories of living and nonliving things. Three complementary cognitive neuropsychological research techniques were employed to assess how, and where, this knowledge is represented in the brain: (i) studies of normal (neurologically intact) subjects, (ii) a case-study of a neurologically impaired patient with a selective deficit in object recognition, and (iii) studies of the anatomical correlates of stored knowledge for living and nonliving things in the brain using magnetoencephalography (MEG).

1.2 BACKGROUND

The dramatic effects of brain damage can provide some of the most interesting insights into the nature of normal cognitive performance. In recent years a number of neuropsychological studies have reported a particular form of cognitive impairment where patients have problems recognising objects from one category but remain able to recognise those from others. The most frequent 'category-specific' pattern is an impairment identifying living things[1] compared to nonliving things (Basso et al, 1988; Caramazza & Shelton, 1998; De Renzi & Lucchelli, 1994; Farah et al, 1989; Forde et al, 1997; Laiacona et al, 1993; Sartori & Job, 1988; Sheridan & Humphreys, 1993; Silveri & Gainotti, 1988; Thomas et al, 2002; Warrington & Shallice, 1984). The reverse pattern of dissociation, i.e., an impairment recognising and naming nonliving things relative to living things, has been reported albeit much less frequently (Cappa et al, 1998; Hillis & Caramazza, 1991; Sacchett & Humphreys, 1992; Silveri et al, 1997; Warrington & McCarthy, 1983; 1987). Using the three aforementioned research techniques this thesis will assess how stored knowledge for categories of living and nonliving things is organised in the brain, in particular, whether different types of knowledge are stored in one homogeneous store, or if stored knowledge can fractionate into a number of functionally and anatomically independent systems. This

[1] The terms living and nonliving things are interchangeable with similar expressions used in the literature, e.g. natural kinds and biological entities for living things, artefacts and man-made items for nonliving things.

introductory chapter will describe the historical and contemporary developments that underpin the work carried out in this thesis in light of research into patients with category-specific deficits for living and nonliving things.

1.3 THEORIES OF CATEGORY-SPECIFICITY

There have been a number of theories proposed to explain category-specific deficits, however, debate continues, and unresolved difficulties remain. Warrington and Shallice (1984) carried out the first empirical study of patients with category-specific impairments. They described the performance of one patient, JBR, who suffered from herpes simplex encephalitis (HSE), which resulted in bilateral temporal lobe damage. As a result, JBR had profound difficulty recognising living things despite relatively normal recognition of nonliving things. For instance, he was only able to recognise 6% of the living things (colour photographs) presented to him, but could recognise 90% of the nonliving things. The authors assessed JBR's deficit in detail and concluded that the impairment was the result of damage to his store of semantic knowledge because, in addition to problems recognising visually presented objects, he was unable to access information about living things from other modalities. For example, JBR was able to give relatively detailed definitions of nonliving things, but he had great difficulty defining living things, often only being able to access general superordinate information (e.g. that a cat is an animal). This was further confirmed by normal performance on visual processing tasks such as matching objects presented in usual and unusual views (Humphreys & Riddoch, 1984).

Since this case there have been numerous reports of patients with category-specific impairments. Like JBR, the majority of patients appeared to have problems accessing stored semantic knowledge (Warrington & Shallice, 1984; Warrington & McCarthy, 1987; Farah & McClelland, 1991), however, some cases have been reported where patients appeared to have problems with early visual processing (Arguin et al, 1996; Funnell, 2000; Thomas et al, 2002), with a pre-semantic structural description system (Humphreys et al, 1988; Riddoch et al, 1988; Sartori & Job, 1988), and with post-semantic/lexical systems (Hart et al, 1985; Farah & Wallace, 1992). In this introductory chapter the studies that led to these different explanations will be reviewed, and the theoretical implications that have arisen as a result discussed.

1.3.1 Confounding Factors

A number of researchers have considered that category-specific impairments emerge due to artefacts that result from experimenter's failure to control for confounding variables such as name frequency, visual complexity and concept familiarity (Funnell & Sheridan, 1992; Stewart et al, 1992). These are warranted concerns and it was evident that early studies in the literature had not controlled for these factors. In light of this, a number of studies reported that category-specific impairments remained even when items were matched for possible confounding variables across categories, and also when *a priori* statistical methods were implemented to account for such confounding effects (e.g. Farah et al, 1996; Forde et al, 1997; Kurbat, 1997; Kurbat & Farah, 1998; Sartori et al, 1993).

1.3.2 Semantic system organised by category

Perhaps the most straightforward explanation for category-specific deficits is that semantic knowledge is categorically organised, i.e., living and nonliving things are implemented in distinct neural structures that can be selectively impaired by focal brain damage (Laiacona et al, 1993; Caramazza et al, 1990; Caramazza & Shelton, 1998). The main evidence supporting this account comes from double dissociations, i.e., from different patients who have impairments for living and nonliving things. Although much more rare than deficits for living things, patients with impairments for nonliving things have been reported on a number of occasions. For example, Hillis & Caramazza (1991) demonstrated a double dissociation between naming living and nonliving things for two patients (using the same stimuli for both). Similarly, Silveri et al (1997) reported data from a patient with a nonliving things deficit using the stimuli from a previous study where a patient had a living things deficit (Sartori et al, 1988). Warrington and McCarthy (1983; 1987) reported data from two patients with problems recognising nonliving things. For example, on a word-picture matching task patient VER performed best with flowers and animals (93% and 86%, respectively), compared to nonliving things (63%). Similarly, patient YOT performed best with animals and flowers (both 86% correct), compared to nonliving things (67%).

However, the categorical explanation suffers in light of evidence from category-specific patients with diffuse rather than focal brain damage (e.g. Gonnerman et al, 1997), and also from diverse functional imaging evidence (see Section 1.4) that

ranges from the involvement of distinct brain areas for the identification of living and nonliving things (e.g. Martin et al, 1996) to a more distributed semantic system (e.g. Devlin et al, 2002). Furthermore, category-specific patients are almost always able to identify some items from the impaired category, and unable to identify others from the spared category. For instance, Warrington and McCarthy (1987) reported that patient YOT had particular difficulties in a task of spoken word-written word matching for small manipulable items. As a result the authors argued that deficits could occur at a more fine-grained level than the usual living-nonliving classification.

Caramazza and Shelton (1998) outlined a categorical account of semantic knowledge that involved separate systems for the recognition of animals, plants, and nonliving things. The authors proposed that evolutionary pressures could have led to an anatomical distinction between the three categories of semantic knowledge both perceptually and semantically, and therefore that there should be patients with impairments for each category. There is little evidence to support this tripartite model in the patient literature. For example, patients are often reported as having impairments for all living things (including animals and plants), but individual deficits for plants and animals are less common, as are impairments for nonliving things; the model outlined by Caramazza and Shelton offered no explanation why one category would more often be impaired than the other two; it predicted equal frequency of impairment for all three. Moreover, other patients have been reported that have a selective deficit for one category (e.g. living things), but that nevertheless have a deficit for specific classes of object within the spared category, for instance, musical instruments and precious stones (Warrington & Shallice, 1984; Silveri & Gainotti, 1988).

1.3.3 Semantic system organised by different types of knowledge: The sensory-functional hypothesis

Many researchers believe that the semantic system is organised by different types of knowledge: namely that the recognition of living things relies more on sensory (or perceptual) properties and the recognition of nonliving things on functional properties (Warrington & Shallice, 1984; Warrington & McCarthy, 1987; Farah & McClelland, 1991). Thus, damage to the sensory system will result in a disproportionate loss of

knowledge about living things and damage to the functional system will result in a disproportionate loss of knowledge about nonliving things.

When they examined JBR's category-specific impairment in more detail, Warrington and Shallice (1984) found it did not clearly delineate living and nonliving categories. For example, he had difficulty defining some nonliving objects, such as precious stones, metals, types of fabric, and musical instruments. As a result the authors argued that semantic memory was organised by particular forms of knowledge – sensory and functional – represented in distinct subsystems. Focal damage to one or other semantic subsystem would result in difficulties identifying items that were differentially dependent on that type of knowledge. Warrington and Shallice proposed that sensory and functional knowledge was differentially important in identifying living and nonliving things respectively. For example, sensory knowledge such as size, shape, colour, and texture is required to distinguish between two living things (such as an apple and an orange), whereas, functional knowledge (what an object is used for, associated with, where it can be found) is necessary to identify nonliving things (such as a hammer or a chair). Therefore, focal damage to the sensory subsystem would not only result in difficulties recognising living things but also nonliving objects that depend on knowledge of sensory information for identification. To illustrate, it is not difficult to imagine that recognition of different fabrics and precious stones requires the retrieval of information about colour and texture.

Warrington and Shallice observed that patients presented with consistent intramodal responses (e.g. when naming pictures, or when defining words); however, there was a lack of intermodal consistency. This dissociation led the authors to propose that input modality, in addition to knowledge type, was a fundamental organising principle of semantic memory because item consistency reflected the degradation of a knowledge store rather than difficulties accessing that store (however, see Forde & Humphreys, 1995 for evidence that item consistency can co-occur with access impairments).

Warrington and McCarthy (1987) developed a model of semantic memory that was more distributed in nature than the original sensory-functional hypothesis. It was based on the ideas of Lissauer (1890) who argued 'the recognition of an object can only occur when at the time of its perception a number of ideas are evoked which

relate to that object. These bring into consciousness those characteristics which the mind has learned to associate with it and those conditions in which it has been previously experienced ... memories laid down through different sensory modalities contribute to these associations but it is only when they are brought into awareness and linked with the percept that the recognition of an object becomes complete'.

Warrington and McCarthy proposed that semantic knowledge is represented in different sensory (visual, tactile, auditory, olfactory) and motor channels that have object-specific weightings associated with them. Therefore, during recognition a multi-channel pattern of activity is generated that is representative of the semantic knowledge we hold for that object. Therefore, as with the sensory-functional hypothesis, living things would tend to have higher weightings in sensory channels and nonliving things in functional and motor channels. However, the multi-modal account moves away from the rigidity of the sensory-functional hypothesis towards a more distributed model of semantic knowledge. For example, the sensory modality may remain highly important in the identification of living things but differential weighting may occur within further subdivisions of that modality (e.g. visual, tactile etc) which in turn may contain differential contributions from further subdivisions (e.g. shape, size, colour for the visual modality). As a result the model would predict that patients with category-specific impairments could also present with more fine-grained deficits that do not necessarily conform to the strict living/nonliving dichotomy. For example, the authors suggested that whereas visual information has a high weighting for both fruit and flowers, colour knowledge would be important for distinguishing between two fruits (e.g. raspberry and blackberry) and shape knowledge would be more relevant for two flowers (e.g. daffodil and tulip). Thus, the model can explain data from patients with category-specific deficits that nevertheless violate the strict living-nonliving dichotomy. For example, a patient able to identify fruit and vegetables was found to have a deficit recognising animals (Hart & Gordon, 1992), and vice versa (Farah & Wallace, 1992).

Furthermore, the model would predict an association between the type of knowledge loss that led to the impairment for particular objects (e.g. colour for fruits) and stored knowledge about colour in general. However, Luzzatti and Davidoff (1994) reported that two patients who successfully named fruits and vegetables presented with

difficulties naming the colour of objects from memory, leading the authors to propose that a problem retrieving the colour of objects across category did not necessarily result in a specific deficit recognising fruit and vegetables. It should be noted in parenthesis that the relative importance of colour for distinguishing between fruits is an intuitive supposition, not an empirically based finding.

The sensory-functional and multi-modal models of the semantic system predict that damage to the sensory system and/or subdivisions within that system will result in a differential impairment for the recognition of living compared to nonliving things and, conversely, that damage to the functional system and/or subdivisions within that system will result in a differential impairment for the recognition of nonliving compared to living things. There are a number of reports of category-specific patients with deficits commensurate with these predictions, but there are also some that are not. Many studies have reported that patients with a category-specific impairment for living things also have a co-occurring deficit for sensory (predominantly visual) features compared to functional features (Basso et al, 1988; Silveri & Gainotti, 1988; Farah et al, 1989; Hart & Gordon, 1992; De Renzi & Lucchelli, 1994; Forde et al, 1997; Humphreys et al, 1997; Moss et al, 1997). In contrast, a number of studies reported that patients with a category-specific impairment for living things showed equivalent levels of difficulty retrieving visual and functional information about living things (Laiacona et al, 1993; Sheridan & Humphreys, 1993; Funnell & De Mornay, 1996; Caramazza & Shelton, 1998). Some studies have reported that patients with a category-specific impairment for living things do not show a corresponding deficit for sensory features (Laiacona et al, 1997; Lambon-Ralph et al, 1998; Moss et al, 1998). Furthermore, Lambon-Ralph et al (1998) reported that patients with a category-specific impairment for nonliving things do not show a corresponding deficit for functional knowledge. These contrasting lines of evidence were integrated in the hierarchical interactive model (HIT) outlined by Humphreys and Forde (2001) (see Section 1.3.7).

1.3.4 Unitary semantic system approach

The limitations of the multiple semantic accounts discussed above have led to an alternative strategy investigating the organisation of semantic knowledge by examining how the features that define living and nonliving things are related. A

number of closely related theories have been formulated with research focusing on three factors 1) feature-type correlations (Caramazza et al, 1990; De Renzi & Lucchelli, 1994; McRae et al, 1997; McRae & Cree, 2002; Gonnerman et al, 1997; Devlin et al, 1998) 2) form-function correlations (Durrant-Peatfield et al, 1997; Moss et al, 1998; Tyler & Moss, 1998), and 3) distinctive feature-types (Garrard et al, 2001; McRae & Cree, 2002).

Feature-type correlations

De Renzi and Lucchelli (1994) proposed that living and nonliving things differ in the links between perceptual and functional features. They argued that stronger correlations exist between the visual and functional features of nonliving compared to living things because visual features such as shape and size are directly related to the function of a nonliving object. Therefore, when perceptual knowledge is degraded nonliving things will be less likely to be impaired than living things, because, although retrieval of perceptual information is equally impaired for all things, the link between perceptual and functional features provides an alternative route to accessing the required knowledge. The nature of this postulated interaction between perceptual and functional features remains unexplained, however. It is unclear how an object's visual appearance could provide the necessary knowledge to allow identification of its function and result in alternative access to recognition if the object cannot be recognised initially. A related account that stresses the importance of the links between perceptual and functional features is the organised unitary content hypothesis (OUCH) model of semantic memory (Caramazza et al, 1990). In this model similar objects share similar features and tend to cluster together in densely populated areas of semantic memory. This results in the differential distribution of items from living and nonliving categories into dense and sparse areas, respectively. The OUCH model predicts that focal damage will produce disproportionate impairments for objects in densely populated areas, which, in turn, can lead to category-specific deficits.

In contrast to research that focused on correlations between perceptual (or sensory) and functional features, McRae et al (1997) examined the correlations within perceptual and functional categories for both living and nonliving things. Subjects were required to generate features for a list of 20 items from both living and nonliving categories. They found a significantly greater amount of functional features were

generated for nonliving compared to living things but no difference between the amounts of perceptual features generated across category. Furthermore, living things tended to have more correlated features than nonliving things, for example, a feature pair such as <has legs-has a tail> was generated across a number of exemplars. The authors proposed that the features of living thing features tend to be more densely correlated than those of nonliving things that tend to have more individualistic and salient features.

The idea that living things have more densely correlated features than nonliving things can account for patterns of performance in category-specific patients with dementia of the Alzheimer's type (DAT). Gonnerman et al (1997) found that DAT patients presented with naming deficits that ranged in severity. The most severe was worse at naming living things and the mildest was worse at naming nonliving things. Perhaps at early stages of DAT when brain damage is diffuse the densely correlated nature of living things support each other, whereas unprotected nonliving things are more vulnerable to damage. In more progressive stages of DAT when generalised brain atrophy is extensive, nonliving things will remain vulnerable, increasing in a linear fashion, and, as the extent of damage becomes less diffuse, impairment for living things will rapidly increase due to damage to correlated features that contribute to the identification of a wide range of category exemplars.

Devlin et al (1998) simulated this pattern of behaviour in a connectionist model of object naming. The authors found that small amounts of indiscriminate damage to the network resulted in difficulty naming nonliving objects. As damage was increased a sharp decline in naming performance was found for living things, and consequently, naming was more difficult for living compared to nonliving things. However, Silveri et al (1991) found that patients with mild to moderate DAT were worse with living compared to nonliving things. Moreover, Garrard et al (1998) found no significant interaction between level of dementia and category-specificity type. Even one of the patients in the DAT group study conducted by Gonnerman et al (1997) presented with a consistent living things impairment. Clearly, the predictions of Gonnerman, Devlin and colleagues cannot be substantiated from the available DAT patient data.

Form-function correlations

Moss and colleagues proposed that features differ between living and nonliving things in terms of 'form-function' correlations (Durrant-Peatfield et al, 1997; Moss et al, 1998; Tyler & Moss, 1998). The authors argued that functional features are important for living as well as nonliving things but they differ in type. For living things, biological actions such as eating and moving are important, whereas for nonliving things an items specific use is most salient. It is in the nature of the correlation between perceptual and functional features that living and nonliving things differ. For living things strong correlations exist between shared perceptual and functional features (e.g. has legs-can move), and within shared perceptual features (e.g. has legs, has feet, has hands, has eyes), and within shared (biological) functional features (e.g. can move, can breathe, can reproduce, can grow). This is different for nonliving things, which have strong correlations between distinctive functional and perceptual features, rather than their shared features (e.g. has blade-used for cutting). The distinctive features of living things (e.g. a zebra's stripes) tend not to have as strong a functional correlate. Therefore, Tyler, Moss and colleagues maintain the idea of correlated perceptual and functional features, however, the nature of the link differs for living and nonliving things. The authors argued that these form-function correlations preserve features following brain damage, however the features are different for living and nonliving things. As a consequence category-specific effects may emerge because, for nonliving things, a strong association between distinctive perceptual and functional features will enable identification (e.g. has a blade-used for cutting – 'axe') but, for living things, a strong link between shared perceptual features and biological function will result in superordinate rather than specific identification (e.g. has legs-can move – 'animal').

Distinctive feature-types

Garrard et al (2001) analysed their data in terms of distinctiveness, i.e., the extent to which a feature allows a particular concept to be distinguished from other members of the same category (Garrard et al, 2001). For example, 'has a trunk' is a distinctive feature of an elephant whereas 'has four legs' is non-distinctive. The authors found that overall there were significantly more distinctive than shared (non-distinctive) features generated. In terms of the S-F theory (Warrington & Shallice, 1984) the distinctive features associated with living and nonliving things should predominantly

be sensory and functional, respectively. Garrard and colleagues found more shared sensory features for living compared to nonliving things, but this was not the case for distinctive features. In general, the prediction of Warrington and McCarthy (1987) that sensory features are crucial for distinguishing among living things, and therefore that damage to visual semantics should result in a category-specific deficit, was not endorsed.

Garrard et al (2001) also examined the influence of shared and distinctive features across categories in terms of feature-pair intercorrelations (e.g. has eyes, can see) and intracorrelations (e.g. has eyes, has head). They found that for living things there was a significantly greater proportion of intercorrelations for shared compared to distinctive features (as proposed by Moss and colleagues), but no difference between the type of correlation. In contrast, for nonliving things there were a significantly greater proportion of intercorrelations for distinctive compared to shared features, and there was a greater proportion of intracorrelations compared to intercorrelations. Overall, however, Garrard et al found that the proportion of significant feature correlations was small (as found by McRae et al, 1997), being made up primarily of intercorrelations among shared features.

Garrard and colleagues argued that their data might explain the disparity in the literature between patients with a deficit for living things, and those few with a nonliving things deficit. They found that the proportion of distinctive features (relative to shared features) generated was greater for nonliving things. The authors argued that such proportions would be maintained if there was generalised, non-selective damage to the brain, and therefore, that the disparity between impairments of living and nonliving things may occur because distinctive features facilitate the recognition of objects more than shared features, particularly in more specific tasks such as object naming.

The Garrard et al study produced similar results to the McRae et al (1997) study; both found a small amount of significant intercorrelations, which were greater for living compared to nonliving things. In terms of the structure of semantic knowledge proposed by Moss and colleagues, Garrard found contrasting results. Support was shown for the proposition that shared perceptual features would be highly correlated

for living things (e.g. has legs, has feet, has hands, has eyes), however, the proposal that there would be a lack of intercorrelation among the distinctive features of living things was not substantiated, in fact, it was not less than any of the features of nonliving things. Furthermore, Garrard et al reported that for nonliving objects the data did not include a significant amount of distinctive, form-function correlations.

1.3.5 Pre-semantic accounts of category-specificity

McCarthy and Warrington (1988) stated, "For a category specific deficit to arise in the first place it is necessary that the information should have already been categorised along a semantic dimension" (p. 428). Recent evidence suggests that this is not the case. A number of studies have presented evidence that category-specific impairments for living things can result from damage to a pre-semantic (Humphreys et al, 1988; Riddoch et al, 1988; Sartori & Job, 1988), or visual processing system (Arguin et al, 1996; Funnell et al, 2000; Thomas et al, 2002). Consistent with semantic accounts of category-specificity, pre-semantic accounts differ in terms of multiple and unitary system organisation.

Structural description system organised by category

Sartori and Job (1988) argued that recognition deficits for a particular category reflected damage to a categorically organised, pre-semantic, structural description system. The structural description system consists of a set of symbolic propositions that describe an objects structure in terms of the configuration of its features or properties. The authors' assertion was based on evidence from a patient, Michelangelo, who presented with a category-specific impairment for living things. Michelangelo had difficulty deciding whether visually presented living things were familiar or not in an object decision test. Object decision is a test that only requires subjects to access the structural description system not (necessarily) semantic knowledge (Riddoch & Humphreys, 1987). Sartori and Job proposed that the structural description system was organised categorically, rather than by knowledge type, because Michelangelo had difficulty specifying the important differences between pairs of visually similar stimuli from the living but not the nonliving category. The authors argued that this finding did not equate with a problem accessing sensory information from the structural description system because, in this case, living and nonliving things should be equally impaired.

Unitary structural description system

Humphreys et al (1988) also argued that damage to a structural description system could result in a category-specific impairment for living things. However, in contrast to Sartori and Job, they proposed a unitary, shared processing system, whereby category-specific impairments would emerge due to the structural similarity between items within the living things category. Humphreys et al (1988) found that when normal subjects list the parts of objects living things tend to have more shared parts than nonliving things. Furthermore, they demonstrated that standardised drawings of living things tend to have a greater magnitude of contour overlap compared to nonliving things. On the basis of these experimental measures Humphreys and colleagues argued that living things have more similar structures to each other than nonliving things - a concept they termed 'structural similarity'.

Humphreys et al (1988) developed a model of object recognition with three levels of representation: (i) the structural description system (ii) semantic representations, (iii) phonological representations. The authors proposed that the structural description system stored the visual properties of objects necessary for identification but not the functional and associative properties, which were represented in the semantic system. The model operates in 'cascade', that is, activation in one stage of the model can be passed on to another before processing has been completed. To illustrate, when an object is viewed (e.g. an apple) structurally similar items (orange, tomato, pear etc) will also be activated, subsequently, the semantic and phonological representations associated with those objects will also be activated. Therefore, activation occurs at all levels of representation before selection of the item in the structural description system. As a consequence, semantic information common to the visual category of the object being viewed is rapidly available prior to individual object recognition. How quickly object identification can occur is dependent on the amount of activated items competing for recognition and this co-varies with semantic activation speed, i.e., an object with many structurally similar neighbours will not be identified quickly due to high competition between them but semantic information will be derived rapidly, conversely, an object with few structurally similar neighbours will be identified quickly but semantic information will not be so rapidly available.

Accordingly, if structurally similar objects tend to be living things and structurally dissimilar tend to be nonliving things, then more visual and semantic competitors will be activated during the identification of living things compared to nonliving things. Consistent with this, Humphreys et al (1988) found that normal subjects took longer to name living compared to nonliving things. Furthermore, Humphreys et al (1998) found that semantic category decisions were made faster for living compared to nonliving things. In addition, Forde et al (1997) reported a case of a patient, SRB, with a category-specific impairment for living things who performed worse at picture naming compared to object decision. Forde et al used regression analysis to show that a measure of structural similarity affected performance more than category, and went on to show that SRB was impaired at distinguishing between a set of structurally similar nonliving objects (different models of car). Interestingly, Gaffan and Haywood (1993) demonstrated that even monkeys found discriminating between pictures of living things more difficult than nonliving things, a finding that led the authors to propose that the observed difference between categories can only be accounted for by the inherent difference in perceptual structure because monkeys are nonverbal animals.

Shape processing differences across categories

Arguin and colleagues (Arguin et al, 1996; Dixon et al, 1997) extended the work of Humphreys and co-workers by outlining the specific visual properties that can lead to processing differences between living and nonliving things. The authors reported the case of a patient, ELM, who presented with a category-specific impairment for living things. On a picture-word matching task ELM tended to confuse structurally similar items (e.g. banana and cucumber). The authors proposed that ELM had difficulty integrating the different structural properties required to differentiate between structurally related objects. They generated a set of stimuli designed to correspond to a three dimensional point in space defined by three structural properties - elongation, tapering, and curvature. For example, a cucumber and carrot correspond in two dimensions (they are elongated and not curved) but they differ on the third (only a carrot is tapered). ELM was presented with four pictures simultaneously displayed in four quadrants, these were removed and another picture was presented centrally. ELM was asked to indicate which quadrant contained the picture that matched the centrally presented picture. He performed better when pictures differed along one dimension

(29% error rate) compared to pictures that differed along two dimensions (57% error rate). As a result, the authors proposed that patient ELM failed to integrate shape information from two dimensions and was better when pictures differed on one dimension because he was only able to attend to one dimension at a time.

Arguin et al demonstrated that this deficit integrating shape information was also affected by semantic similarity between items. ELM was required to name presented shapes as semantically related living things (fruit and vegetables) in one block and as semantically unrelated nonliving things in another. ELM performed worse at naming fruit and vegetables from a conjunction set compared to a single dimension set. However, the effect of dimensionality was not found when he was required to name nonliving things. This contrast in performance across category could only be explained by the semantic properties attributed to the items because the same shape sets were used in both living and nonliving conditions. Humphreys et al (1988) showed that semantically related living things tend to be structurally similar to each other whereas the opposite is the case for nonliving things. Consistent with this, Arguin et al suggested that structurally similar living things are more semantically related to each other compared to the semantic closeness between structurally similar nonliving things. Accordingly, the authors argued that semantic distance contributes to the integration of structural information about structurally similar objects, and as a consequence, can result in selective recognition impairments for living things.

1.3.6 Post-semantic accounts of category-specificity

Some authors have reported patients with category-specific impairments that appeared to be the result of damage to a post-semantic system, for example, in tests of name retrieval (Cappa et al, 1998; Farah & Wallace, 1992; Forde et al, 1997; Hart et al, 1985; Humphreys et al, 1997). For instance, Farah and Wallace (1992) reported that patient TU could categorise items as living things (fruit and vegetables) but he was selectively impaired at naming them (see Hart et al, 1985; Forde et al, 1997; Humphreys et al, 1997 for the same pattern of results). As a result, the authors proposed that TU had a category-specific anomia, rather than a visual agnosia or semantic impairment, because he had similar difficulty naming visually and verbally presented living things, and could retrieve a large amount of semantically related information about the items he could not name. Cappa et al (1998) reported that

patient GP had a deficit naming nonliving things, with the sub-category tools being the most severely affected. GP had a largely preserved semantic knowledge about those items he could not name. Therefore, a number of case studies have demonstrated that category-specific effects can be observed in patients with lexical retrieval difficulties, without significant concomitant semantic impairment.

Consistent with these data, Humphreys et al (1997) reported two patients with category-specific naming impairments for living things who could not name living items, but had access to semantic knowledge about the same items, for example, they could successfully categorise fruit and vegetables. In addition to this, Humphreys and colleagues demonstrated that both patients had problems in tests of object decision, drawing from memory, and naming (living and nonliving things) from perceptual definitions; all tasks that required access to stored visual knowledge. Humphreys et al (1997) argued that this seemingly contradictory finding of intact access to semantic knowledge from vision, and a deficit in visual knowledge might have reflected the role of top-down activation of visual knowledge during object naming, and incorporated the idea into the Hierarchical Interactive Theory (HIT) of category-specificity, which is outlined in the following section.

1.3.7 The Hierarchical Interactive Theory (HIT) – A unified account?

Thus far, this introduction has described the theories proposed to explain category-specific deficits. In general, they can be distinguished in terms of the damaged system (pre-semantic, semantic, post-semantic), and how that system is organised (multiple or unitary). However, in a recent report Humphreys and Forde (2001) attempted to unify the various accounts of category-specificity in their hierarchical interactive theory (HIT). The HIT has the same two defining characteristics as the cascade model of object naming (Humphreys et al, 1988, see Section 1.3.5): (1) a hierarchical architecture of stored representations, and (2) partial activation is sufficient for the transfer of information between different processing stages. Therefore, selective damage can occur to each stage in the model without any of the other stages necessarily being damaged.

There is some neuropsychological evidence to support this type of architecture. For instance, some patients perform well on tests that require access to stored structural

knowledge (e.g. object decision), but have difficulties matching objects that are related in a non-perceptual associative manner (e.g. car and road) (Hillis & Caramazza, 1995; Humphreys & Riddoch, 1999; Sheridan & Humphreys, 1993). As previously outlined, Sartori and Job (1988) found that their patient Michelangelo had difficulty with object decisions, particularly for the affected category (living things) (see also Caramazza & Shelton, 1998). In contrast, some patients perform well on object decision, even for the affected category (Laiacona et al, 1997; Sheridan & Humphreys, 1993). These data suggest that selective deficits for living things can result from damage to distinct functional stages of object recognition: the structural description system and a later semantic or lexical system.

The Cascade model (Humphreys et al, 1988) can accommodate all these deficits due to the feed-forward nature of its architecture, however, it cannot accommodate impairments that involve top-down or re-entrant mechanisms such as those proposed to be involved during object naming (see Section 1.3.7). In order to incorporate impairments of this kind, Humphreys and Forde (2001) developed the HIT to include an interactive component. They incorporated re-entrant feedback processing in the HIT in terms of an interactive and competitive framework (see e.g. Humphreys et al, 1997). Humphreys and Forde proposed that during the initial processing of objects stored structural descriptions would be activated, as well as partial activation of semantic (associative/functional) knowledge. They argued that additional (re-entrant) activation of visual knowledge is required so that perceptually similar objects can be differentiated, and as a result, the name of the object could be determined. Therefore, for patients with category-specific anomia such as those described by Humphreys et al (1997), initial activation of semantic knowledge would occur, but because of their visual knowledge deficits, there would be little or no re-entrant activation of visual information, resulting in these patients being unable to differentiate between a set of semantically and visually related objects.

The explanation of category-specific impairments for living things is the same in the HIT as in the Cascade model, i.e., greater visual similarity between living things results in more competition between living than nonliving exemplars. This competition is continued downstream in semantic and lexical systems and results in slower name retrieval for living compared to nonliving things. In addition to this,

Humphreys and Forde suggested that damage to stored visual knowledge might affect living more than nonliving things because living things rely more on perceptual information for recognition than nonliving things. For example, the colour or shape of a fruit is more diagnostic than the colour or shape of a tool, which may rely more on object associated actions such as the movement pattern associated with a hammer. Furthermore, the aforementioned strong correlations between the sensory (perceptual) and functional features of living things (e.g. McRae et al, 1997; Moss et al, 1997; see Section 1.3.4) would affect nonliving things less than living things, because more perceptual features are associated with living things, and therefore they are more prone, probabilistically, to damage.

On the basis of evidence from the functional imaging literature on category-specificity (see Section 1.4 and Chapter 5), Humphreys and Forde (2001) suggested that inferior occipito-temporal regions of the brain would be involved in re-entrant activation of visual knowledge. In addition, they argued that re-entrant activation might also benefit the recognition of certain nonliving things. For instance, Warrington and McCarthy (1987) proposed that object associated actions may be useful for distinguishing between different tools. Humphreys and Forde suggested that the inferior left frontal gyrus and the temporal-occipital-parietal junction may be involved in re-entrant activation of sensori-motor knowledge, and therefore the recognition of nonliving things (e.g. see Martin et al, 1996; Damasio et al, 1996).

Clearly, the HIT has a framework for explaining the varied neuropsychological data from the category-specific literature. There are two critical aspects to this framework: (1) that there is a hierarchical architecture of stored representations, and (2) that re-entrant activation benefits recognition. The former point ensures that each stage of the model can be selectively spared when the other stages are damaged. For example, it can explain how patients with selective deficits to stored visual knowledge have no corresponding impairment with other forms of stored knowledge (e.g. Sheridan & Humphreys, 1993). The latter point provides a theoretical basis for evidence from the functional imaging and lesion based literature concerning the areas of the brain that are involved in recognising living and nonliving things, evidence which is considered in the following section. In summary, the strength of the HIT lies in its explanatory power; it can account for the various category-specific effects that have been

documented over many years of investigation. Consistent with this, Humphreys and Forde argued that category-specific impairments for living and nonliving things can arise from a number of distinct functional loci, and that dependent on the task, stored visual and functional (specifically action-related) knowledge may be recruited on-line during the object recognition process.

1.4 THE NEURAL CORRELATES OF CATEGORY-SPECIFICITY

As outlined above there have been numerous investigations of patients with category-specific deficits, which, in turn, have led to the development of a number of related functional models of category-specificity. In contrast, the neuroanatomical correlates of category-specificity are less well developed. This section describes the recent developments in both lesion and functional imaging research.

1.4.1 Lesion Studies

Many studies that have reported category-specific deficits for living things have involved patients with herpes simplex encephalitis (HSE). In these cases a general consistency in anatomical location of lesion can be asserted. HSE typically causes bilateral damage to the temporo-limbic structures and can extend to non-limbic structures within the temporal lobe, in particular the inferior temporal cortices (see Gainotti et al, 1995). Indeed, using structural MR scans, a number of studies have found consistent lesion sites in the temporal cortices for HSE patients with category-specificity (De Renzi & Luchelli, 1994; Sartori & Job, 1988; Sirigu et al, 1991; Warrington & Shallice, 1984). In addition, category-specific deficits for living things have been found in group studies involving patients with dementia of the Alzheimer's type (DAT) (Mazzoni et al, 1991; Silveri et al, 1991; Giustolisi et al, 1993). These studies also permit an assertion regarding consistency of lesion site because it is common early in the course of DAT that temporo-limbic structures are damaged.

Two group studies of patients with category-specific deficits for living or nonliving things reported contrasting results. Damasio et al (1996) reported that deficits naming animals were associated with unilateral damage to the left inferior (predominantly anterior) temporal cortex, whereas a deficit naming tools was associated with damage to the postero-lateral inferior temporal cortex, and the junction of temporal, occipital, and parietal cortices. Tranel et al (1997) reported that deficits recognising animals

were associated with bilateral damage to the medial occipito-temporal cortex, whereas a deficit recognising tools was associated with the left junction of occipital, temporal, and parietal cortices. The two studies differ in the task employed: namely patients were required to name and recognise items in the Damasio et al and Tranel et al studies, respectively. It is not unexpected to find that lesion sites associated with naming animals were anterior to those associated with recognising them (see e.g. Levelt et al, 1998) but conclusions along these lines should be tentative.

Gainotti et al (1995) reviewed the patients in the literature with category-specific impairments for nonliving things. The number of studies is limited and the types of nonliving categories that are impaired varies between patients as indeed does the nature of the spared living categories, nevertheless, there is a good deal of consistency with lesions generally affecting the left fronto-parietal regions. Furthermore, Gainotti et al concluded that patients with category-specific impairments for living things have, in general, lesions in bilateral antero-medial temporal lobe areas and inferior temporal regions.

In general, evidence from lesion studies suggests that recognition and naming of living and nonliving things is associated with distinct neural regions. Damage to left temporal regions, in particular, inferior and medial areas are associated with a living things deficit, whereas damage to left fronto-parietal regions is associated with a nonliving things deficit. However, divergent cases exist where patients with a category-specific impairment for living things have left fronto-parietal lesions (Caramazza & Shelton, 1998; Laiacona et al, 1993). The lesion-based approach has a number of well-recognised limitations. For example, lesions rarely conform to functionally distinct neuroanatomical systems. Patients can display reorganisation or recovery of function that can vary over time and be dependent upon variables such as age and gender. Another interpretative complication concerns premorbid neurological and psychiatric factors, such as epilepsy, schizophrenia, and so forth. In addition, a lesion can result in loss of function not because it interferes with the specific information-processing task of a given structure but because it interrupts fibres of passage to and from areas crucial for function. Therefore, with lesion studies one can only conclude that the damaged region was necessary for the lost cognitive function not that it was sufficient for, or uniquely associated with the lost function.

Functional brain imaging techniques have several advantages over the lesion deficit model and can supplement neuropsychological attempts to understand the neural correlates of cognitive functions. These techniques allow for non-invasive measurement of brain activity in normal subjects (as well as patients) and as a result can be used to identify those brain areas that sustain particular tasks (e.g. cognitive, sensory, motor). Furthermore, the whole brain can be observed rather than attention being restricted to a particular damaged cortical region. Described in the following section are some recent studies that have investigated the neural correlates of category-specificity using functional imaging techniques (for a more detailed assessment of all the functional imaging studies of category-specificity see Section 5.2).

1.4.2 Functional Brain Imaging Studies

In the first published functional imaging study of category-specificity, Perani et al (1995) used positron emission tomography (PET) to compare the areas of the brain that were activated when normal subjects performed a same-different visual recognition task on line drawings of living things (animals) and nonliving things (manipulable objects, e.g. computer mouse, sports racket). Increased activation was found in left fusiform and left lingual gyri for animals relative to manipulable objects, and in the left inferior frontal gyrus for objects relative to animals.

Martin et al (1996) reported similar results to Perani et al. They used PET to compare activation when subjects named line drawings and silhouettes depicting either living things (animals) or nonliving things (tools). They found bilateral but greater activation in the left medial occipital region (including the left lingual gyrus) and left inferior temporal lobes for the naming of animals relative to tools, and in the left middle temporal gyrus, left inferior frontal region and left premotor regions for the naming of tools relative to animals. Martin et al reported that their finding of differential activation in the left middle temporal gyrus when naming tools was similar to areas that were activated when subjects named objects associated with actions (Wise et al, 1991; Martin et al, 1995), and activation in the left premotor area was similar to areas activated when subjects imagined grasping objects (Decety et al, 1994). Damasio et al (1996) also used PET to examine neural activation when subjects named line

drawings of animals and tools. However, on the basis of their analysis of the lesion sites of category-specific patients the authors restricted the area of interest to the ventral temporal cortex. They found that animals activated left inferior middle temporal cortex (an area more anterior than that found by Martin et al, 1996), and tools activated left posterior middle temporal cortex (the same area found by Martin et al).

Cappa et al (1998) carried out a PET investigation into the effects of semantic category and knowledge type (see also Mummery et al, 1998 for a similar study). Subjects were visually presented with words of living or nonliving things and asked to retrieve visual and functional/associative information about each word. For example, whether an animal had a short or long tail accessed visual knowledge, whether it was native to a certain country accessed associative knowledge. Cappa and colleagues found increased activity in the left temporo-occipital junction region for nonliving things, irrespective of the task used (the same area activated in all the PET studies discussed thus far). In addition, judgements made about nonliving things also showed differential activation in left supramarginal gyrus, the right superior temporal gyrus, and the right thalamus. Living things increased activation in the right middle frontal gyrus and the right fusiform gyrus, again irrespective of the task used.

One problem with these PET studies was that the stimuli tended not to be matched across the living and nonliving items used (typically, animals and tools). Therefore, it might have been the case that the observed category differences were actually due to confounding factors such as visual complexity or item familiarity. Moore and Price (1999) addressed this issue in a PET study using pictures of living (animals and fruits) and nonliving things (vehicles and tools). They attempted to separate category effects from effects due to differences in the visual configuration of objects by comparing the stimuli across four groups: 1) multicomponent living things (animals), 2) multicomponent nonliving objects (e.g. vehicles), 3) living things with simple shapes (fruit and vegetables), and 4) nonliving objects with simple shapes (e.g. tools). One group of subjects named the pictures, another made same-different judgements about whether picture-word pairs were from the same category. For multicomponent compared to simple shaped objects, the right occipito-temporal, fusiform and medial extrastriate cortices were activated. In this latter area, strongest activation was found

for multicomponent nonliving objects (vehicles). In the two former areas, activity was strongest for multicomponent living things (animals) and least for simple nonliving objects (tools), and there was more activity for multicomponent nonliving compared to simple nonliving things.

Left posterior temporal cortex was differentially activated for nonliving things, but only in the picture-word matching task. In both tasks, for nonliving things, increased activation was observed in left medial extrastriate cortex (left lingual gyrus), an area previously associated with the reverse comparison (Perani et al, 1995; Martin et al, 1996). Left lingual gyrus activation was most prominent for vehicles relative to animals, but there was also significant activation for animals relative to fruit and vegetables. The authors argued that the findings reflected the visual configuration of the items used (vehicles being the most visually complex, fruits being the least) rather than an implicit category difference. For living things increased activation was found bilaterally in anterior temporal regions extending into the insula, and the right posterior middle temporal gyrus for both tasks, but only for black and white drawings; when appropriate colouring was added the effects were eliminated. The authors concluded that the ease with which an object can be identified (structurally and semantically) is critical in determining which areas of the brain will be active, and therefore, category specific differences can be attributable to the different demands placed on the processing of objects (such as structural complexity) rather than implicit differences in semantic category.

In a similar study, Gerlach et al (1999) used PET to examine cortical activity during an object-decision task. The real objects were either living or nonliving and the task differed in difficulty in the amount of perceptual differentiation needed to perform it, i.e., a non-object using novel parts constituted an easy decision, one using the component parts of the real objects constituted a difficult decision. When task difficulty was easy no category differences were found, however, as task difficulty increased a differential increase in activation for living compared to nonliving things was found in the right inferior temporal and anterior fusiform gyri. The authors interpreted this finding as reflecting the greater perceptual differentiation required for recognising living compared to nonliving things, and argued that category effects can arise at a pre-semantic level distinct from semantic processing.

Studies using functional magnetic resonance imaging (fMRI) have also been used to look for differences in cortical activity when subjects identify living and nonliving things. For instance, Thompson-Schill et al (1999) used fMRI to examine activity when subjects answered verbally presented questions about the visual and nonvisual attributes associated with living and nonliving things. They restricted the areas of interest to ventral occipito-temporal cortex due to a declared interest in the fusiform gyrus as a site of importance for the retrieval of visual information. Thompson-Schill et al found increased activation in the fusiform gyrus when subjects answered visual questions about living and nonliving things, as well as nonvisual questions about living things, but not for nonvisual questions about nonliving things. They argued that their findings confirmed the role played by the fusiform gyrus in retrieval of visual semantic knowledge (as previously shown by D'Esposito et al, 1997; Martin et al, 1995). The authors argued that the fusiform gyrus was associated with the retrieval of visual knowledge regardless of category, and also when living things are processed, regardless of question-type. As a result the authors proposed that, in the fusiform gyrus they identified an area of the brain that showed differential activity dependent on modality, i.e., the recognition of living things depended on access to stored visual knowledge, regardless of the task.

Chao et al (1999) used fMRI to examine activity for living and nonliving things during picture naming, picture matching, picture viewing and reading object names. For pictures of tools increased activation was found bilaterally in the medial fusiform gyrus and the lateral middle posterior temporal gyrus. Similarly, for the reading task, there was consistent activation in the left posterior middle temporal gyrus for tools. For pictures of animals increased activation was observed in bilateral medial and inferior occipital, ventral temporal and superior temporal cortices (for all pictorial tasks). In contrast, there was no activity in the medial occipital gyrus during the reading task, and all the other regions of activity found during the pictorial tasks were inconsistently replicated across subjects. For example, 2/8 and 3/8 subjects showed significant activity in the left and right inferior occipital gyrus, respectively. Similarly, 4/8 and 5/8 subjects showed significant activity in the left and right lateral fusiform gyrus, respectively.

Leube et al (2001) used fMRI to examine neural activity when subjects were asked to categorise items as either living or nonliving things. Increased activation was observed for living things in the right fusiform gyrus, middle temporal and inferior frontal regions. No significant difference in activation was observed for nonliving relative to living things. The right hemispheric activations during processing of the living category in this study were at variance with results from the aforementioned PET studies that found predominantly left hemispheric activation (e.g. Damasio et al, 1996 and Martin et al, 1996). However, these PET studies examined lexical retrieval using pictorially presented animals and tools. Leube et al argued that it was likely that naming animals and answering questions about their properties is cognitively different from a living-nonliving categorisation task, which focuses much more on features of the objects that are critical for distinguishing among these categories, i.e., features that define the living category.

Devlin et al (2002) investigated the neural correlates of category-specificity using both PET and fMRI. They conducted three experiments; in the first they used PET to examine the activity associated with making lexical decisions (deciding whether a visually presented word was real or not) about items from four categories (animals, fruit, tools, and vehicles). The authors found no significant differences between any of the four categories or between living and nonliving things grouped together. Devlin et al carried out a second PET experiment using a categorisation paradigm (living-nonliving) to increase the demands on the semantic system (the lexical task required activation of semantic and phonological regions whereas the categorisation task required only semantic activation). Again, no significant effects between living and nonliving things were found. In a third experiment Devlin et al replicated the categorisation experiment, this time using fMRI to increase the spatial resolution, however, no significant differences in activation were found. The authors concluded that their data provided evidence that semantic knowledge is represented in a distributed neural system, undifferentiated by category or feature-type, as opposed to being segregated in neural systems dedicated to different domains.

In summary, the functional imaging studies of category-specificity produced a diverse set of findings, with little between-study consensus concerning the cortical areas involved. The most consistent finding was activation of the left middle temporal gyrus

for nonliving things relative to living things. The next most consistent finding was activation of the left inferior frontal gyrus for nonliving compared to living things. However, consistencies were few and far between, and they were often observed in studies that employed different paradigms and/or used different stimuli (see Section 5.2 for a detailed assessment of all the functional imaging studies on category-specificity carried out to date).

1.5 OVERVIEW OF THE THESIS

This introductory chapter has described the influential cognitive neuropsychological evidence relating to explanations of category-specific effects, and why they emerge following brain damage. The disparate nature of the evidence discussed provides a framework for the specific investigations carried out in the following chapters. For each chapter a detailed assessment of the research relevant to the issues under investigation will be reported.

In Chapter 2 an experiment into the organisation of category-specific knowledge in normal subjects will be reported. In particular, this chapter will examine the relationship between feature knowledge and category structure by analysing the feature norms generated by normal subjects in a semantics definitions experiment.

In Chapter 3 a case study of a patient with a category-specific impairment for living things will be reported that documents the effects of time on stored semantic knowledge. The work in this chapter has been published in Neurocase (Thomas et al, 2002).

In Chapter 4 two case studies will be reported that examined the role of local and global processing in category-specific visual agnosia. In particular, the visual recognition impairments of each patient will be examined to test if their visual agnosia could have led directly to their category-specific deficit for living things. In addition, this chapter provided a framework for understanding the role of local and global processing in visual object recognition. The work in this chapter has been submitted to Neurocase.

In Chapter 5 an investigation into category-specific object recognition in the human brain using MEG will be reported. The experiments in this chapter were designed to investigate the neural correlates of different categories of knowledge; and here for the first time MEG will be used to evaluate whether there are category-specific brain areas. The results will allow the predictions from the different models of category-specificity outlined in this introduction to be assessed.

Finally, in Chapter 6 the empirical objectives and findings will be summarised and discussed in terms of how the work carried out in this thesis has extended our current understanding of category-specificity.

CHAPTER 2

A FEATURE-NORM INVESTIGATION OF CATEGORY-SPECIFICITY

2.1 INTRODUCTION

As outlined in the previous chapter a number of strategies have been formulated to investigate the nature of category-specific semantic deficits[2] by examining the features that define living and nonliving things, and how they are related to each other (Section 1.3.4). The empirical research has focused on three factors 1) feature-type analysis (e.g. Farah & McClelland, 1991; McRae & Cree, 2002), 2) feature correlations (e.g. Garrard et al, 2001; McRae et al, 1997, McRae & Cree, 2002; Devlin et al, 1998; Durrant-Peatfield et al, 1997), and 3) distinguishing feature-types (e.g. McRae & Cree, 2002). The primary aim of this chapter was to examine the relationship between feature knowledge and category structure by analysing feature norms generated by subjects in a semantic definition experiment. These data were used to assess theories of category-specificity that maintain the importance of different properties (e.g. sensory-functional), for different categories, and to provide a sufficient quantity of feature norms to permit basic-level categories to be considered (e.g. animals, birds, tools, vehicles) as well as the usual higher-level category (living-nonliving). The method of analysis employed was comprehensive, using four feature-based techniques: 1) feature-types, 2) core features, 3) distinctive versus shared features, and 4) feature correlations.

In terms of the theoretical models outlined in Chapter 1, this chapter is limited to addressing *semantic* models of category-specificity by using feature-norm investigations. However, this is just one part of a complementary set of experimental chapters that each address different aspects of the many proposed models of category specificity. For instance, chapters 3 and 4 explicitly address non-semantic theories of category-specificity not investigated here. Prior to the experimental investigations the following section reviews the literature that has used feature-norms as a basis for investigating category-specificity.

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[2] These studies were only concerned with the organisation of *semantic* knowledge, patients in the literature reported as having non-semantic category-specific deficits (see Section 1.2.3 and DW in chapters 4 and 5) were not considered.

Feature-types analysis

As discussed in the previous chapter (Section 1.3.3) category-specific deficits have often been explained in terms of damage to semantic systems organised by different types of knowledge (Warrington & Shallice, 1984; Warrington & McCarthy, 1987). However, there is still a lack of independent empirical evidence to support these theories. Attempts have been made to investigate the feature-types associated with living and nonliving things but the methods used to collect and analyse the data are varied and the results are inconclusive. For instance, Farah and McClelland (1991) had twenty subjects read dictionary definitions of 48 living and 48 nonliving things taken from the items used by Warrington and Shallice to test patients with category-specificity (1984, Experiment 2). Subjects were asked to underline each occurrence of visual (10 subjects) and functional features (10 subjects). Functional features were defined as 'what the item does or what it is for'. The authors found that visual features were greater in number for both living and nonliving things, however the proportions differed. The ratio of visual to functional features was 7.7:1 for living things and 1.4:1 for nonliving things (see Table 2.1).

Subsequent to the Farah and McClelland (1991) study, researchers have questioned what type of features should be used as the basis of analysis. For example, whether only visual or all sensory features (e.g. visual, tactile, auditory, taste/smell) should be taken into account, and also, how a functional feature should be defined. For instance, the definition of functional has ranged from a narrow definition (e.g. what an object is used for) to a much wider one (e.g. what an object is used for, who uses it, and where, when and how it is used). Caramazza and Shelton (1998) suggested that subjects in the Farah and McClelland study might have been reluctant to classify functional information for living things because asking what an object is for (i.e., a functional question) is more natural for nonliving things. They argued that asking subjects to identify sensory and nonsensory (rather than functional) features would reduce the bias and in turn the ratios. Caramazza and Shelton replicated the experiment using the same stimuli and procedure used by Farah and McClelland except subjects were requested to underline either all sensory features (8 subjects) or all nonsensory features (8 subjects). They found the ratios to be very similar for both categories; 1.2:1 for living things, and 1:1 for nonliving things, a finding, the authors argued,

showed the method of analysis used by Farah and McClelland failed to provide an empirical foundation for the sensory-functional hypothesis.

Devlin et al (1998) carried out a feature-norms analysis using the same definition of functional features as Farah and McClelland, but like Caramazza and Shelton they also calculated features for sensory (visual, auditory, or tactile) rather than just visual features. Devlin et al asked 30 subjects to generate as many sensory and functional features for 60 presented words (30 living, 30 nonliving). Overall, there were more sensory than functional features generated (88 and 57 respectively). The authors found the same pattern of results as Farah and McClelland (1991) but it was less prominent, with a ratio of 3:1 for living things, and 1.4:1 for nonliving things.

Table 2.1. Feature-type ratios for living and nonliving things.

Study	Comparison	Living	Nonliving
Farah & McClelland	Visual-Functional	7.7:1	2.8:1
Caramazza & Shelton	Sensory-Nonsensory	1.2:1	1.0:1
Garrard et al	Sensory-Functional (F-M)	2.0:1	1.6:1
Garrard et al	Sensory-Nonsensory	1.2:1	1.2:1
Devlin et al	Sensory-Functional	3.0:1	1.4:1
McRae	Visual-Functional (narrow)	5.6:1	1.5:1
McRae	Sensory-Functional (narrow)	6.4:1	2.2:1
McRae	Sensory-Functional (F-M)	2.1:1	1.9:1
McRae	Sensory-Functional (wide)	1.8:1	1.4:1
McRae	Sensory-Nonsensory	0.8:1	0.8:1

Note: F-M was the Farah and McClelland functional definition. The narrow functional definition was 'what an object is used for'. The wide functional definition was 'what an object is used for, who uses it, and where, when and how it is used'. The sensory definition included visual, tactile, taste/smell, and auditory features. The nonsensory definition included all features that were not sensory (e.g. functional, encyclopaedic).

Garrard et al (2001) also replicated the Farah and McClelland feature-type experiment, and found similar but not as striking results. They used a cued semantic production experiment (e.g. a cat has... a cat can... a cat is...). Twenty subjects were asked to fill in the blanks for 64 items selected from the standardised set of Snodgrass and Vanderwart (1980) items. Garrard and colleagues found that the sensory to functional (Farah & McClelland definition) ratio was 2:1 for living things and 1.6:1 for nonliving things, a difference they demonstrated was statistically significant. When sensory features were compared against nonsensory features (functional and

encyclopaedic), the ratios for living and nonliving things were the same (1.2:1). The lack of an interaction between feature-type and category when nonsensory features were included in the analysis replicated the findings of Caramazza and Shelton (1998) and, the authors argued, provided evidence against the sensory-functional hypothesis, at least in terms of the different proportions of sensory and functional features.

McRae and Cree (2002) (see also McRae et al, 1997) replicated the feature-norm collection method used by Devlin et al, using the same number of subjects (30), but with a significantly larger amount of items (206 living and 343 nonliving things). Furthermore, they calculated feature-types using a wide range of sensory and functional definitions (see Table 2.1). McRae and Cree found that feature-type differed significantly across category only when the functional definition was narrow (i.e., what an item is used for). For visual relative to functional (narrow) they found a ratio of 5.6:1 and 1.5:1 for living and nonliving things, respectively. Similarly, for sensory relative to functional (narrow) they found a ratio of 6.4:1 and 2.2:1 for living and nonliving things, respectively. All other comparisons yielded no significant differences.

Owing to the large number of items in their database, McRae and Cree were able to consider the ratios of basic-level categories that are subsumed within the living-nonliving distinction (e.g. birds, vehicles, insects, weapons). They found that living things (especially creatures) tended to pattern together with high sensory-functional ratios, as did nonliving things with much lower ratios, whereas other items from both superordinate categories were situated in the middle with similar ratios (e.g. fruit, food, plants, vehicles). McRae and Cree (2002) argued that their analyses showed that feature-type discriminated between living and nonliving categories, but only when the functional definition was narrow; when all semantic information was included (or even just when the functional definition was widened, as Farah and McClelland) this effect disappeared. Therefore, they concluded that a theory of semantic organisation excluding the vast majority of nonsensory was flawed, and the question of whether feature-type distribution can provide insight into category-specific deficits remained open (McRae & Cree, 2002).

Distinctive feature-types

Garrard et al (2001) analysed their feature-norm data in terms of distinctiveness, i.e., the extent to which a feature allows a particular concept to be distinguished from other members of the same category (Garrard et al, 2001). For example, 'has a trunk' is a distinctive feature of an elephant whereas 'has four legs' is non-distinctive. The authors found that there were more distinctive features generated for nonliving things than living things (mean = 5.7 and 4.9 per item for nonliving and living things, respectively).

Devlin et al (1998) found the same result when they calculated the distinctive features from their feature-norm database (they termed these 'informative features'; mean = 3.4 and 2.4 per item for nonliving and living things, respectively). Furthermore, McRae and Cree (2002) found the corresponding result with their much larger feature-norm database (mean = 5.2 and 3.2 per item for nonliving and living things, respectively). As a result, McRae and Cree proposed that the greater number of distinctive features for nonliving things could explain why the majority of patients reported in the literature present with a category-specific impairment for living things, compared to the few with nonliving deficits. For example, if there was generalised, non-selective damage to the brain, the disparity between impairments of living and nonliving things may occur because distinctive features facilitate the recognition of objects more than shared features, particularly in more specific tasks such as object naming.

In addition, Garrard et al (2001) argued that the S-F theory would predict that those distinctive features associated with living things would be largely sensory and those associated with nonliving things largely functional. Following the overall feature-type analysis, Garrard et al examined the distribution of distinctive and shared features in two conditions: 1) sensory-functional (F-M), and 2) sensory-nonsensory. They found that there were significantly more distinctive sensory than functional features, but this difference disappeared when nonsensory features were included in the analysis. Furthermore, they found shared (non-distinctive) sensory features were more numerous for living compared to nonliving things, but this was not the case for distinctive features. Therefore, the prediction of Warrington and McCarthy (1987) that sensory features are crucial for distinguishing among living things, and that

damage to visual semantics should result in a category-specific deficit, was not endorsed.

Features correlations

For over twenty-five years researchers have investigated the role of feature correlations in the structure of semantic concepts (Keil, 1987, 1989; Malt & Smith, 1984; Rosch, 1978; Rosch et al, 1976). Keil (1989) found that semantic features were often correlated with each other (intercorrelated), in particular for living things (see also Malt & Smith, 1984). For example, a bird that has feathers is also likely to have a beak, two legs, and a tail. Using their feature-norm data, McRae et al (1997) provided evidence that feature intercorrelations are important for semantic processing. They calculated the Pearson product moment correlation across 190 basic-level concepts (76 living, 114 nonliving) and found that there were more intercorrelated features for living compared to nonliving things (although this was a nonsignificant pattern due to the small number of correlations found overall). McRae and Cree (2002) extended this analysis to include data from 206 living and 343 nonliving concepts and found a more robust, significant difference with the features of living things more densely intercorrelated than those of nonliving things. This evidence that correlated features were important for encoding semantic information, and were different for living and nonliving things, led researchers to investigate their role in category-specific deficits.

Devlin et al (1998) also assessed the role played by feature correlations in their model of category-specificity, which was designed to account for the deficits of patients with dementia of the Alzheimer's type (DAT). For example, Gonnerman et al (1997) found that DAT patients presented with naming deficits that ranged in severity. The most severe was worse at naming living things and the mildest was worse at naming nonliving things. They argued that at early stages of DAT when brain damage is diffuse the densely correlated nature of living things support each other, whereas unprotected nonliving things are more vulnerable to damage. In more progressive stages of DAT when generalised brain atrophy is extensive, nonliving things will remain vulnerable, increasing in a linear fashion and, as the extent of damage becomes less diffuse, impairment for living things will rapidly increase due to damage to correlated features that contribute to the identification of a wide range of category exemplars. Devlin et al (1998) simulated this pattern of behaviour in a connectionist

model of object naming. The authors found that small amounts of indiscriminate damage to the network resulted in difficulty naming nonliving objects because there were less correlated features for nonliving things to provide compensatory activation when individual features were disrupted. As damage was increased a sharp decline in naming performance was found for living things, and consequently, naming was more difficult for living compared to nonliving things. However, Silveri et al (1991) found that patients with mild to moderate DAT were worse with living compared to nonliving things. Moreover, Garrard et al (1998) found no significant interaction between level of dementia and category-specificity type. Even one of the patients in the DAT group study conducted by Gonnerman et al (1997) presented with a consistent living things deficit. Clearly, the correlated feature model of category-specificity of Gonnerman, Devlin and colleagues cannot be substantiated from the available DAT patient data.

An alternative model of category-specificity was developed that emphasised the importance of feature correlations, however, in contrast to the Devlin et al model, Moss and colleagues (Durrant-Peatfield et al, 1997; Moss et al, 1997, 1998; Tyler & Moss, 1997) argued that the type of correlated features were different for living and nonliving things. They proposed that features differ between living and nonliving things in terms of 'form-function' correlations, and that the functional features are in turn different for living and nonliving things. For instance, biological actions such as eating and moving are important functional features for living things, whereas an items specific use is most salient for nonliving things. It is in the nature of the correlation between sensory and functional features that living and nonliving things differ. For living things strong correlations exist between shared sensory and functional features (e.g. has legs-can move), and within shared sensory features (e.g. has legs, has feet, has hands, has eyes), and within shared (biological) functional features (e.g. can move, can breathe, can reproduce, can grow). This is different for nonliving things, which have strong correlations between distinctive functional and sensory features (e.g. has blade-used for cutting). The distinctive features of living things (e.g. a zebra's stripes) tend not to have strong functional correlates.

Therefore, Moss and colleagues maintained the idea that correlated features were important in the underlying organisation of semantic knowledge, however, they

suggested that the nature of the link differed for living and nonliving things. The authors argued that these form-function correlations preserve features following brain damage, however the features are different for living and nonliving things. As a consequence, category-specific effects for living things may emerge because, for nonliving things, a strong association between distinctive sensory and functional features could enable identification (e.g. has a blade-used for cutting – 'axe') but, for living things, a strong link between shared perceptual features and biological function would maintain superordinate rather than specific identification (e.g. has legs-can move – 'animal'). Interestingly, the predictions concerning the pattern of category-specific impairments for DAT patients were opposite to those of Gonnerman et al and the Devlin et al model. Moss et al predicted that with mild to moderate damage, category-specific impairments for living things would emerge because nonliving things would be 'protected' by the sensory-functional correlation between distinctive features. However, with very severe damage to semantic knowledge patients might be better at identifying living things. As discussed earlier, this is opposite to Devlin and colleagues who argued that mild damage would result in a deficit for nonliving things because the features associated with living things were more densely correlated, and therefore preserved, whereas more extensive damage resulted in a crossover to a relative deficit for nonliving things because intercorrelated features tended to fail en masse.

Garrard et al (2001) also examined the influence of shared and distinctive features across categories in terms of feature-pair intercorrelations (e.g. has eyes, can see) and intracorrelations (e.g. has eyes, has head). They found that for living things there was a significantly greater proportion of intercorrelations for shared compared to distinctive features (as proposed by Moss and colleagues), but no difference between the type of correlation. In contrast, for nonliving things there was a significantly greater proportion of intercorrelations for distinctive compared to shared features, and there was a greater proportion of intracorrelations compared to intercorrelations. Overall, however, Garrard et al found that the proportion of significant feature correlations was small (as found by McRae et al, 1997), being made up primarily of intercorrelations among shared features.

The Garrard et al study produced similar results to the McRae et al (1997) study; both found a small amount of significant intercorrelations, which were greater for living compared to nonliving things. For Garrard et al less than 90% of correlations were significant, however, it was possible that this was due to the small number of concepts used (64). In terms of the structure of semantic knowledge proposed by Moss and colleagues, Garrard et al found contrasting results. Support was found for the proposition that shared perceptual features would be highly correlated for living things (e.g. has legs, has feet, has hands, has eyes), however, the proposal that there would be a lack of intercorrelation among the distinctive features of living things was not substantiated, in fact, it was not less than any of the features of nonliving things. Furthermore, Garrard et al reported that for nonliving objects the data did not include a significant amount of distinctive, form-function correlations.

The motivation for producing a feature-norm database in the present study was to examine the relationship between feature knowledge and category structure. The size of the database allowed the relationship between basic-level categories to be considered, as well as the usual living-nonliving distinction. Moreover, the data permitted empirical evaluation of theories of category-specificity that maintain the importance of different properties (e.g. Warrington & Shallice, 1984; Warrington & McCarthy, 1987), and the relationship between those different properties (e.g. Devlin et al, 1998; Durrant-Peatfield et al, 1997), for different semantic categories.

2.2 EXPERIMENTAL INVESTIGATIONS

One difficulty assessing the aforementioned feature-norm studies was the variation in the number of items from living and nonliving categories. This ranged from a relatively small sample of 30 living and 30 nonliving things (Devlin et al), to 48 for both categories (Caramazza & Shelton), in fact only McRae and colleagues (McRae et al, 1997; McRae & Cree, 2002) collected a large amount of feature norms (76 living things and 114 nonliving things in the former study, growing to 206 living things and 343 nonliving things in the latter). The experiment in this chapter was designed to replicate and extend the McRae et al work by using a large number of exemplars (180) from eleven different basic-level categories subordinate to the living-nonliving classification (see Appendix A). The items were chosen from the Snodgrass and Vanderwart (1980) standardised set of line drawings, which are used in almost all the

studies on category-specificity. The extensive number of items used enabled a detailed and more reliable investigation into the features-types generated for different categories normally subsumed within the living-nonliving taxonomy. This will allow future researchers to generate definitions of living and nonliving things that are matched for difficulty, for example, in terms of feature frequency. The data were analysed in terms of four feature-based theories of semantic organisation, i.e., feature types, core features, distinguishing features, and feature correlations.

2.2.1 Method

One hundred subjects aged between 18 and 45 years participated (mean age = 22.1 years). The stimuli consisted of 180 items from the Snodgrass and Vanderwart (1980) set. Four living object categories (animals, birds, insects, fruit and vegetables) and five nonliving categories (vehicles, furniture, tools, kitchen items, and clothing) were used (see Appendix A). Two further categories (musical instruments and body parts) were included but not categorised as either living or nonliving due to evidence from patients with category-specific impairments suggesting they do not fit into the living-nonliving taxonomy (Warrington & Shallice, 1984). Five sets of stimuli were created with an equal number of category types distributed within each set, thus each subject was presented with an approximately equivalent number of items Each subject was presented with a printed document consisting of the written names of one of the five sets of stimuli and requested to give written definitions in the space provided for each target stimuli. Subjects were asked to write the definitions in sentence form rather than lists of features.

For analysis, subject responses were recoded into individual components of information (e.g. 'a mouse can be white or brown' was split up into 'a mouse is white' and 'a mouse is brown'). Synonymous information was also recoded (e.g. 'an alligator is dangerous' was grouped with 'an alligator is vicious'). In common with previous studies (McRae et al, 1997; Garrard et al, 2001) features generated only once were not included within the analysis. The proportion of subjects that generated a particular feature was calculated (maximum of 20), and each generated feature-type was categorised using the following classification system:

1) Superordinate (e.g. orange – fruit, pliers - tool)
2) Functional (an objects use, e.g. kettle – boiling water; cow – meat, milk)

3) Visual (a property predominantly determined from vision, e.g. elephant – big ears, apple – green)
4) Tactile (a property predominantly determined by touch, e.g. peach – soft skin, beetle – hard shell)
5) Auditory (a property predominantly determined by hearing, e.g. cat – purrs, clock – ticks)
6) Taste/smell (a property predominantly determined by tasting or smelling, e.g. strawberry – sweet tasting, cheese – strong smell)
7) Associated action (an action associated with an object, e.g. hammer – strike things, frog - hops)
8) 'Like a' (e.g. a zebra is like a horse)
9) Other (features not readily fitting into the above categories)

2.2.2 Results

The following items were excluded from the analysis: bear, bow, glasses, nail, nut, pepper, and stool. This exclusion was either a result of an incorrect interpretation of ambiguous exemplars by more than 20% of subjects (e.g. nail <found on end of the finger> as opposed to the item struck with a hammer) or an accidental omission by the subject. Hence, 173 items remained in the analysis of which 74 were living things, 76 nonliving things, 10 musical instruments, and 13 body parts. Each item was defined by a maximum of 20 subjects. The number of features generated for each target item was calculated resulting in a total of 2028 at a mean of 11.72 features per item. The total number of features generated for the category of living things was 945 at a mean of 12.77 per item, for the category of nonliving things it was 842 at a mean of 11.08 features per item. A one-way ANOVA showed that there was a significant difference between the number of features generated for living and nonliving categories [$F(1, 149) = 13.96$, $p<0.01$].

Feature-types analysis

The aim of the feature-type analysis was to assess the fundamental claim of the S-F hypothesis, i.e., that semantic knowledge about living and nonliving things is differentially encoded in terms of sensory and functional features, respectively. In addition, the distribution of feature-types in nine basic-level categories within the living-nonliving taxonomy (and musical instruments and body parts) was assessed.

This latter analysis allowed the type of sensory and functional features that underpin knowledge of particular categories to be assessed. For instance, as outlined in Section 1.3.3, Warrington and McCarthy (1987) proposed that semantic knowledge is represented in different sensory (visual, tactile, auditory, olfactory) and motor channels that have object-specific weightings associated with them. For example, the authors suggested that whereas visual information would be important for both fruit and flowers, colour knowledge would be important for distinguishing between two fruits (e.g. raspberry and blackberry) and shape knowledge would be more relevant for two flowers (e.g. daffodil and tulip, see also Breedin et al, 1994; Humphreys & Forde, 2001).

The following analysis assessed the features associated with living and nonliving things in five ways, (1) assessment of feature type using a visual and functional (narrow) classification (using all features listed as functional in Appendix A; as used by Farah & McClelland, 1991), (2) using a visual and functional (wide) classification (all features listed as functional and associated action in Appendix A) (3) using a sensory (all features listed as visual, tactile, auditory, smell/taste in Appendix A) and functional (narrow) classification (as used by Caramazza and Shelton, 1998), (4) using a sensory and functional (wide) classification, and (5) assessment of feature types using sensory and non-sensory (all features listed in Appendix A other than sensory; as used by McRae & Cree, 2002). Table 2.2 shows the number of features generated for each basic-level category in terms of the classification outlined above.

Table 2.2. All generated feature-types across the eleven basic-level categories.

Basic-level category	SUP	FUN	VIS	TAC	AUD	T/S	AA	LIK	OTH	TOTAL
Animals	78	19	185	29	14	1	27	10	122	**485**
Birds	17	3	49	0	4	0	16	0	25	**114**
Body Parts	15	19	46	0	0	0	1	0	48	**129**
Clothing	24	19	91	1	0	0	3	7	74	**219**
Fruit and vegetables	29	23	102	15	0	23	4	2	63	**261**
Furniture	18	19	57	3	1	0	7	3	28	**136**
Insects	11	0	36	2	3	1	12	0	20	**85**
Kitchen Items	41	33	69	6	0	0	12	2	27	**190**
Musical Instruments	13	4	47	1	9	0	7	3	28	**112**
Tools	20	26	64	6	0	0	8	3	28	**155**
Vehicles	14	22	41	1	0	0	17	3	44	**142**
TOTAL	**280**	**187**	**787**	**64**	**31**	**25**	**114**	**33**	**507**	**2028**

Living and nonliving things

Table 2.3 shows each feature-type ratio for all five conditions for living and nonliving things. For the visual-functional (narrow) comparison a ratio of 7.7:1 for visual features (total = 379) relative to functional features (total = 49) for living things, and a ratio of 2.8:1 for visual features (total = 325) relative to functional features (total = 117) for nonliving things was found. The data were analysed using a between-items ANOVA with category (living-nonliving) and feature-type (visual-functional (narrow)) the factors. A main effect of feature-type [$F(1, 296) = 419.54$, $p<0.01$] and a significant interaction between category and feature-type [$F(1, 296) = 22.78$, $p<0.01$] was found.

For the visual-functional (wide) comparison a ratio of 3.7:1 was found for visual features (total = 379) relative to functional features (total = 102) for living things, and 2:1 for visual features (total = 325) relative to functional features (total = 165) for nonliving things. A main effect of feature-type [$F(1, 296) = 240.08$, $p<0.01$] and an interaction between category and feature-type [$F(1, 296) = 17.94$, $p<0.01$] was found. These findings showed the same pattern as the previous comparison, hence, no

difference was found when the functional definition was widened to include associated action features.

Table 2.3. Feature-type ratios for living and nonliving things.

Comparison	Living	Nonliving
Visual-Functional (narrow)	7.7:1	2.8:1
Visual-Functional (wide)	3.7:1	2.0:1
Sensory-Functional (narrow)	9.5:1	3.0:1
Sensory-Functional (wide)	4.6:1	2.1:1
Sensory-Nonsensory	1:1.1	1:1.5

For the sensory-functional (narrow) comparison a ratio of 9.5:1 for sensory features (total = 465) relative to functional features (total = 49) for living things, and a ratio of 3:1 for sensory features (total = 345) relative to functional features (total = 117) for nonliving things was found. As with the previous two comparisons a main effect of feature-type [$F(1, 296) = 239.33$, $p<0.01$] and an interaction between category and feature-type [$F(1, 296) = 21.04$, $p<0.01$] was found.

For the sensory-functional (wide) comparison a ratio of 4.6:1 was found for sensory (total = 465) relative to functional features (total = 102) for living things, and of 2.1:1 for sensory (total = 345) relative to functional features (total = 165) for nonliving things. Once again, a main effect for feature-type [$F(1, 296) = 311.12$, $p<0.01$] and an interaction between category and feature-type [$F(1, 296) = 19.47$, $p<0.01$] was found. Therefore, when sensory rather than visual information was included in the analysis the findings were the same regardless of the functional definition used.

Finally, for the sensory-nonsensory comparison the present analysis found a ratio of 1:1.1 for sensory features (total = 465) relative to nonsensory features (total = 506) for living things, and a ratio of 1:1.5 for sensory features (total = 345) relative to nonsensory features (total = 515) for nonliving things. The ANOVA produced a main effect of category [$F(1, 296) = 70.44$, $p<0.01$], and feature-type [$F(1, 296) = 30.08$, $p<0.01$] and a significant interaction between category and feature-type [$F(1, 296) = 9.63$, $p<0.01$]. Therefore, when all feature information was included in the analysis there was a significant difference between the number of features generated for living and nonliving things (living more than nonliving), and for feature-types (nonsensory more than sensory), and critically the interaction between feature-type and category

remained, i.e., for both living and nonliving things there was a greater amount of nonsensory features but the number of sensory features generated was significantly greater for living things.

Basic-level categories

The size of the feature database generated by subjects in this chapter allowed the features associated with basic-level categories subsumed within the living-nonliving taxonomy to be investigated. Owing to the similarity in the previous section between comparisons of visual-functional and sensory-functional features, the following analysis included sensory-functional (narrow), sensory-functional (wide), and sensory-nonsensory feature comparisons.

Table 2.4 shows the feature-type ratios for each of the eleven basic-level categories across the three feature conditions. The distribution of feature-types for basic-level categories were very similar to that found for living and nonliving things. For the comparison between sensory and functional (narrow) features, creatures (animals, birds, insects) tended to be grouped together with very high S-F ratios. In contrast, nonliving things were also grouped together but with much lower ratios. In the middle was the fruit and vegetable category; a non-creature group of living items. The ratios for musical instruments and body parts were more indicative of living and nonliving things, respectively.

Table 2.4. Basic-level category feature-type ratios in descending order for a) sensory-functional (narrow), b) sensory-functional (wide), and c) sensory-nonsensory.

a)

Category	Basic-level category	S-F (narrow)
Living	Insects	41:0
Living	Birds	17.7:1
	Musical Instruments	14:1
Living	Animals	12:1
Living	Fruit and vegetables	5.3:1
Nonliving	Clothing	4.6:1
Nonliving	Furniture	3.3:1
Nonliving	Tools	2.7:1
	Body Parts	2.3:1
Nonliving	Kitchen Items	2.1:1
Nonliving	Vehicles	2.1:1

b)

Category	Basic-level category	S-F (wide)
	Musical Instruments	5.6:1
Living	Animals	5.0:1
Living	Fruit and vegetables	4.6:1
Nonliving	Clothing	4.0:1
Living	Insects	3.4:1
Living	Birds	2.8:1
Nonliving	Furniture	2.5:1
	Body Parts	2.2:1
Nonliving	Tools	2.1:1
Nonliving	Kitchen Items	1.6:1
Nonliving	Vehicles	1.2:1

c)

Category	Basic-level category	S-NS
Living	Fruit and vegetables	1:1
Living	Animals	1:1.1
Living	Insects	1:1.1
Living	Birds	1:1.2
Nonliving	Tools	1:1.2
Nonliving	Clothing	1:1.4
Nonliving	Kitchen Items	1:1.6
	Musical Instruments	1:1.8
	Body Parts	1:1.8
Nonliving	Furniture	1:2.2
Nonliving	Vehicles	1:2.2

For the comparison between sensory and functional (wide) features, a very similar pattern of results was found, albeit with reduced ratios throughout. The category of clothing was the only set that strayed outside its superordinate group, overtaking insects, which in turn had a striking decrease from the highest ratio in the previous analysis to the lowest living things ratio when the functional definition was widened.

In general, widening the functional definition reduced the ratios for all categories, but the creature sets were affected more than nonliving things and fruit and vegetables. Again, musical instruments and body parts showed a pattern in accord with living and nonliving categories, respectively. As found in the previous condition, vehicles and kitchen items were the nonliving categories with the smallest ratios.

For the comparison between sensory and nonsensory features, a further reduction in the ratios was found compared to the previous two conditions, however, the same grouping of living and nonliving basic-level categories was found. Again, the creature categories were closely grouped, as were all nonliving categories. The fruit and vegetables category continued its rise from having the smallest ratio when sensory features were compared to functional (narrow) features, to the only category with a 1:1 ratio when sensory features were compared to nonsensory features.

2.2.3 Discussion

The results from the feature-type analysis were consistent with previous research that found a difference in the ratio of visual/sensory and functional features for living and nonliving things (e.g. Farah & McClelland, 1991). Importantly, this pattern emerged even when all nonsensory features were compared with sensory features. This is inconsistent with some studies that showed no difference in ratios of sensory and nonsensory features for living and nonliving things (e.g. Caramazza & Shelton, 1998), and perhaps it could be accounted for by the larger number of items used in the present experiment.

The results from the more detailed analysis of individual categories showed a pattern similar to the overall living-nonliving distinction. In particular, creatures tended to have similar visual-functional (sensory-nonsensory) ratios to each other across each condition, but appeared to some extent to be independent of the fruit and vegetable category, which varied in position across condition. Fruit and vegetables was the living category with the smallest ratio when the functional information was narrow, and the biggest ratio when all nonsensory features were included. Items from nonliving categories showed comparable ratios to each other throughout, the greatest difference was between clothing and vehicles, which represented the two extremes. Therefore, although there was some patterning of basic-level categories into distinct

groups they tended to remain within their superordinate category. The exception to this was musical instruments and body parts, which were more indicative of living and nonliving things, respectively. This finding is consistent with the literature on category-specific impairments, which shows that patients who have deficits in either living or nonliving things also tend to have deficits for musical instruments and body parts, respectively (e.g. Warrington & Shallice, 1984).

The tripartite distinction between creatures, fruit and vegetables, and nonliving things corresponds to some deficits of category-specific patients reported. For example, cases have been reported where patients are particularly impaired at naming fruit and vegetables (Farah & Wallace, 1992; Hart et al, 1985), and where patients have a deficit for animals alone (Caramazza & Shelton, 1998; Hart & Gordon, 1992). The tripartite pattern also has implications for the domain-specific hypothesis (Caramazza and Shelton, 1998; see Section 1.3.2). Caramazza and Shelton argued against a feature-based explanation of category-specificity and proposed that evolutionary pressures resulted in the development of specialised neural regions for the representation of three different categories: animals, plant life, and artefacts. The present results supported the view of a system differentiated by these three categories, but rather than being the result of damage to specialised neural systems organised by category, impairments for animals, plants, or artefacts could result from damage to stored sensory or functional (nonsensory) knowledge.

The differences between basic-level categories are interesting in terms of the distributed model of semantic memory (Warrington & McCarthy, 1987 see 1.3.3 see also Humphreys & Forde, 2001 Section 1.3.7). The model predicted that category-specific impairments could occur for basic-level categories within living or nonliving groups because different types of fine-grained knowledge would be important for different items. For instance, specific deficits for animals or fruit and vegetables could result from damage to stored sensory knowledge, but at a more fine-grained level, with animals being differentially reliant on shape information, and fruit and vegetables on taste or texture. Although a more detailed analysis of features with a larger number of items would be required to assess any differences between these more fine-grained sensory features, the present analysis appeared to provide initial supportive evidence. For instance, 23 features classified as 'taste/smell' were

associated with fruit and vegetables compared to only one for animals, and 14 features classified as 'auditory' were associated with animals compared to none for fruit and vegetables (see Table 2.2).

In summary, the results from the feature-type analyses found a distinction between the types of features generated for both living and nonliving things, and for basic-level categories within the living-nonliving classification. This was the case when sensory features were compared to functional (narrow and wide definitions), and when sensory features were compared to all nonsensory features. Therefore, these data supported the fundamental claim of the S-F hypothesis that semantic knowledge about living and nonliving things is principally encoded in terms of sensory and functional features, respectively.

2.2.4 Core feature analysis

In the previous feature-type analysis (Section 2.2.2) all features were included regardless of the number of times features were generated by the group of subjects (e.g. any number between 2 and 20). For example, for 'elephant' the feature <has trunk> generated by all twenty subjects was essentially equivalent to the feature <scared of mice> generated by only two subjects. Clearly, some features are more central or important in our representations of objects and the aim of this section was to analyse their 'core' features in more detail. A core feature was defined as a property generated by at least half the subjects (10 or more) for a single item. The concept of a core feature is new to this field or research, with none of the aforementioned feature-based studies having used it as a method of investigation.

Living and nonliving things

The number of core features generated for each item was calculated resulting in a total of 480 at a mean of 2.77 per item. The total number of core features generated for living things was 242 (mean of 3.27 per item), for nonliving things it was 187 (mean of 2.46 per item). A one-way ANOVA showed that there was a significant difference between the number of core features generated for living and nonliving things [$F(1, 149) = 11.53$, $p<0.01$]. Table 2.5 shows the number and type of core features for each basic-level category.

Table 2.5. All generated core feature-types across the eleven basic-level categories.

Basic-level category	SUP	FUN	VIS	TAC	AUD	T/S	AA	LIK	OTH	TOTAL
Animals	30	6	49	7	3	1	8	4	19	**127**
Birds	8	1	5	1	0	0	2	0	4	**21**
Body Parts	2	7	3	0	0	0	1	0	12	**25**
Clothing	11	9	10	0	0	0	2	1	20	**53**
Fruit and vegetables	21	3	33	1	0	4	2	0	9	**73**
Furniture	5	7	8	0	0	0	3	2	1	**26**
Insects	7	0	9	0	0	1	3	0	1	**21**
Kitchen Items	7	18	14	1	0	0	4	1	2	**47**
Musical Instruments	8	1	11	0	2	0	2	0	2	**26**
Tools	4	16	13	0	0	0	3	0	1	**37**
Vehicles	3	6	8	0	0	0	2	0	5	**24**
TOTAL	**106**	**74**	**163**	**10**	**5**	**6**	**32**	**8**	**76**	**480**

The following core feature analysis included sensory-functional (narrow), sensory-functional (wide), and sensory-nonsensory comparisons. Table 2.6 illustrates each feature-type ratio for the three conditions for living and nonliving things. For the sensory-functional (narrow) comparison a ratio of 11.4:1 was found for sensory relative to functional features for living things, and 1:1.1 for sensory relative to functional features for nonliving things. A main effect of core feature-type [$F(1, 148) = 47.54$, $p<0.01$] and a significant interaction between category and core feature-type [$F(1, 148) = 55.22$, $p<0.01$] was found.

For the sensory-functional (wide) comparison a ratio of 4.6:1 was found for sensory relative to functional features for living things, and 1:1.3 for sensory relative to functional features for nonliving things. A main effect of core feature-type [$F(1, 148) = 22.94$, $p<0.01$] and an interaction between category and core feature-type [$F(1, 148) = 50.95$, $p<0.01$] was found. These findings were the same as the previous condition, hence, no difference was found when the functional definition was widened to include core associated action features.

Table 2.6. Core feature-type ratios for living and nonliving things.

Condition	Living	Nonliving
Sensory-Functional (narrow)	11.4:1	1:1.1
Sensory-Functional (wide)	4.6:1	1:1.3
Sensory-Nonsensory	1:1.1	1:2.5

Finally, for the sensory-nonsensory comparison a ratio of 1:1.1 was found for sensory features relative to nonsensory for living things, and 1:2.5 for sensory features relative to nonsensory features for nonliving things. The ANOVA produced a main effect of category [$F(1, 148) = 11.53$, $p<0.01$], and core feature-type [$F(1, 148) = 32.15$, $p<0.01$] and a significant interaction between category and core feature-type [$F(1, 148) = 15.03$, $p<0.01$]. Therefore, when all core features were included in the analysis there was a significant difference between the number generated for living and nonliving things (living more than nonliving), and for feature-types (nonsensory more than sensory), and critically the interaction between feature-type and category remained, i.e., the difference in the number of sensory and nonsensory core features generated for nonliving things was significantly larger (53 compared to 135) than it was for living things (114 compared to 129).

Basic-level categories

Table 2.7 shows the core feature-type ratios for each of the eleven basic-level categories across the three feature conditions. For the comparison between sensory and functional (narrow) features, living categories were grouped together, as were nonliving categories, but the latter had much lower S-F ratios than the former. This distinction between living and nonliving categories was also found when all features were included but here it appeared to be even clearer. The ratios for musical instruments and body parts were more indicative of living and nonliving things, respectively.

Table 2.7. Basic-level category core feature-type ratios in descending order for a) sensory-functional (narrow), b) sensory-functional (wide), and c) sensory-nonsensory.

a)

Category	Basic-level category	S-F (narrow)
	Musical Instruments	13:1
Living	Fruit and vegetables	12.7:1
Living	Insects	10:0
Living	Animals	10:1
Living	Birds	6.0:1
Nonliving	Vehicles	1.3:1
Nonliving	Clothing	1.1:1
Nonliving	Furniture	1.1:1
Nonliving	Tools	1:1.2
Nonliving	Kitchen Items	1:1.2
	Body Parts	1:2.3

b)

Category	Basic-level category	S-F (wide)
Living	Fruit and vegetables	7.6:1
Living	Animals	4.3:1
	Musical Instruments	4.3:1
Living	Insects	3.3:1
Living	Birds	2.0:1
Nonliving	Vehicles	1:1
Nonliving	Clothing	1:1.1
Nonliving	Tools	1:1.5
Nonliving	Kitchen Items	1:1.5
Nonliving	Furniture	1:1.3
	Body Parts	1:2.6

c)

Category	Basic-level category	S-NS
Living	Fruit and vegetables	1.1:1
	Musical Instruments	1:1
Living	Insects	1:1.1
Living	Animals	1:1.1
Nonliving	Tools	1:1.8
Nonliving	Vehicles	1:2.0
Nonliving	Kitchen Items	1:2.1
Nonliving	Furniture	1:2.3
Living	Birds	1:2.5
Nonliving	Clothing	1:4.3
	Body Parts	1:8.3

For the comparison between sensory and functional (wide) features, a very similar pattern of results was found, albeit with reduced ratios throughout. No category strayed outside its superordinate group, but the distance between the two extreme living and nonliving categories (birds and vehicles) decreased. Again, musical instruments and body parts showed a pattern of results in accord with living and nonliving categories.

For the comparison between sensory and nonsensory features, a further reduction in the difference between ratios was found compared to the previous two conditions, however, the same grouping of living and nonliving basic-level categories was found with the exception of the category birds, which fell from being the living category with the smallest ratio in the previous two conditions to a position in the middle of the group of nonliving categories.

2.2.5 Discussion

Core features showed the same pattern as the overall feature-type analysis for living and nonliving things, i.e., there was a distinction between the types of features generated for living and nonliving things, both when core sensory features were compared to core functional features (narrow and wide definitions), and when core sensory features were compared to all nonsensory core features. However, it was noticeable that living and nonliving things were more tightly grouped within their respective categories, and there was more distance between the two categories. This was particularly the case for the two sensory-functional comparisons. Therefore, it would appear that core features have a higher probability of being sensory and functional for living and nonliving things, respectively.

In contrast to the overall feature-type analysis for basic-level categories, core features did not find as distinct a difference between creatures, fruit and vegetables, and nonliving things. However, living categories and nonliving categories remained grouped, with the one exception of birds in the sensory-nonsensory comparison. This difference was due to the reduced number of core features compared to the number of all features. In particular, when all features were included there was a clear difference between the two sensory-functional comparisons for creatures and fruit and vegetables; the former tended to have more associated action features than functional features, and the latter the opposite pattern. This was not the case for core features, where both creatures and fruit and vegetables had very few functional and associated action features between them (see tables 2.2 and 2.5).

2.2.6 Distinctive and shared features analysis

The results from both feature-types analyses provided an insight into the organisation of semantic knowledge about living and nonliving things and showed that visual

(sensory) knowledge and functional (nonsensory) knowledge tended to be more important for living and nonliving things, respectively. The data also showed that subjects tend to generate more features for living things, however, it offered no explanation in terms of how this organisation could be disrupted and result in category-specific deficits. Thus far, the only prediction based on feature-type and core features could be that because there are significantly more living features in both cases then mild, indiscriminate damage would result in living features being less vulnerable to loss than nonliving features. Distinctive features may be more informative because tasks that assess category-specific effects typically require subjects to distinguish between similar items. For instance, when asked to identify a picture of a tiger, a subject might recognise that it has four legs, a tail, and is shaped like a big cat. This information may be necessary for successful identification, but it would not be sufficient to discriminate the tiger from other big cat pictures; for this the subject needs to recognise that it has stripes. Hence, distinctive features are critical for object identification and it was the initial aim of this section to assess the proportion of distinctive (and shared) features generated for living and nonliving things. The second aim was to assess whether distinctive and shared feature-types also tended to be sensory and functional for living and nonliving things, respectively.

In this section a distinctive feature was defined as one generated in less than three basic-level items within a category (e.g. animals), and by at least half the subjects (10 and above). For example, for the item 'elephant' all twenty subjects generated the feature <has trunk> and it occurred only once across all basic-level items in the animal category. In contrast, a shared feature was defined as a non-distinctive feature, i.e., a feature generated in greater than two basic-level items within a category, and by at least half the subjects. For example, for the item 'pumpkin' seventeen subjects generated the feature <is orange> which occurred in three other basic-level items within the fruit and vegetable category (orange 20 subjects; carrot 17 subjects; peach 2 subjects). Therefore, in this latter case peach was not included in the analysis because less than half the subjects generated the feature <is orange>.

Living and nonliving things

Figure 2.1 shows the mean number of distinctive and shared features for living and nonliving things. A two (living-nonliving) by two (distinctive-shared) between-items

ANOVA revealed main effects for category [F (1, 296) = 22.43, $p<0.01$], and distinctive/shared [F (1, 296) = 55.62, $p<0.01$], as well as an interaction [F (1, 296) = 66.09, $p<0.01$]. Therefore, there were significantly more distinctive features generated for nonliving (total = 91) compared to living things (total = 65), and conversely, significantly more shared features generated for living (total = 177) compared to nonliving things (total = 87). Tables 2.8 and 2.9 show the number and type of distinctive and shared features, respectively, for each basic-level category.

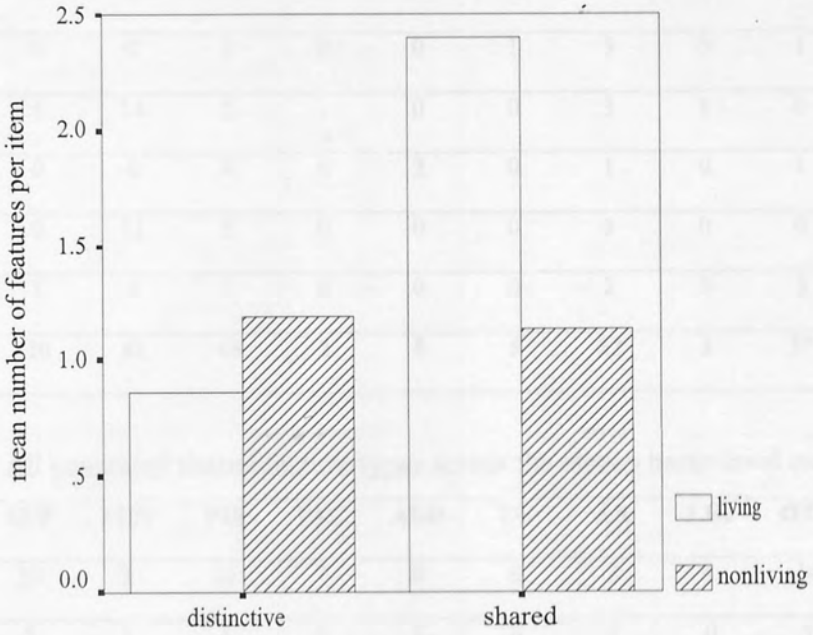


Figure 2.1. The mean number of distinctive and shared features generated for living and nonliving things.

Table 2.8. All generated distinctive feature-types across the eleven basic-level categories.

Basic-level category	SUP	FUN	VIS	TAC	AUD	T/S	AA	LIK	OTH	TOTAL
Animals	2	5	12	1	3	1	4	0	8	**36**
Birds	2	0	3	0	0	0	1	0	3	**9**
Body Parts	1	8	3	0	0	0	0	0	7	**19**
Clothing	2	5	3	0	0	0	1	1	11	**23**
Fruit and vegetables	1	1	4	0	0	3	0	0	3	**12**
Furniture	0	7	4	0	0	0	4	1	0	**16**
Insects	0	0	3	0	0	1	3	0	1	**8**
Kitchen Items	1	14	5	1	0	0	3	1	0	**24**
Musical Instruments	0	0	4	0	2	0	1	0	1	**8**
Tools	0	11	5	0	0	0	3	0	0	**19**
Vehicles	1	1	2	0	0	0	2	0	3	**9**
TOTAL	**10**	**52**	**48**	**2**	**5**	**5**	**22**	**3**	**37**	**184**

Table 2.9. All generated shared feature-types across the eleven basic-level categories.

Basic-level category	SUP	FUN	VIS	TAC	AUD	T/S	AA	LIK	OTH	TOTAL
Animals	30	3	35	7	0	0	3	1	14	**93**
Birds	5	1	2	0	0	0	1	0	1	**10**
Body Parts	1	0	2	0	0	0	0	0	1	**4**
Clothing	10	4	7	0	0	0	0	0	8	**29**
Fruit and vegetables	20	2	28	1	0	1	2	0	6	**60**
Furniture	4	0	6	0	0	0	0	0	0	**10**
Insects	7	0	6	0	0	0	1	0	0	**14**
Kitchen Items	6	1	10	0	0	0	0	0	2	**19**
Musical Instruments	8	1	8	0	0	0	0	0	0	**17**
Tools	5	1	8	0	0	0	0	0	1	**15**
Vehicles	4	4	4	0	0	0	0	0	2	**14**
TOTAL	**100**	**17**	**116**	**8**	**0**	**1**	**7**	**1**	**35**	**285**

The following feature-types analysis assessed the distinctive and shared features associated with living and nonliving things in the same way as in the previous section, i.e., using a sensory-functional (narrow), a sensory-functional (wide), and a sensory-nonsensory classification. Table 2.10 shows each distinctive and shared feature-type ratio for all three conditions for living and nonliving things.

Table 2.10. Feature-type ratios for living and nonliving things, a) distinctive features, b) shared features.

a)

Distinctive features condition	Living	Nonliving
Sensory-Functional (narrow)	5.2:1	1:1.9
Sensory-Functional (wide)	2.2:1	1:2.6
Sensory-Nonsensory	1:1.1	1:3.6

b)

Shared features condition	Living	Nonliving
Sensory-Functional (narrow)	13.3:1	3.5:1
Sensory-Functional (wide)	6.2:1	1.5:1
Sensory-Nonsensory	1:1.2	1:1.5

In the following three feature comparisons a two (e.g. sensory-functional) by two (distinctive-shared) by two (living-nonliving) between-items ANOVA was used. For the sensory-functional (narrow) comparison there were significantly more shared than distinctive features [$F(1, 296) = 10.44$, $p<0.01$], in addition to main effects produced for feature-type (sensory more than functional) [$F(1, 296) = 82.23$, $p<0.01$], and category (living more than nonliving) [$F(1, 296) = 4.21$, $p<0.05$].

In addition, an interaction between feature-type and distinctive/shared was found [$F(1, 296) = 58.27$, $p<0.01$], i.e., distinctive and shared features differed in terms of their ratio of sensory-functional features, which was greater for the latter (see Table 2.10). There was also an interaction between feature-type and category [$F(1, 296) = 59.99$, $p<0.01$], i.e., living and nonliving things differed in terms of their ratio of sensory-functional features, which was greater for the former. The ANOVA revealed a final interaction between category and distinctive/shared [$F(1, 296) = 27.61$, $p<0.01$], i.e., distinctive and shared features differed in terms of the proportion of features generated for living and nonliving things; there were more shared features for living

compared to nonliving things, and conversely, more distinctive features for nonliving compared to living things (see Figure 2.2).

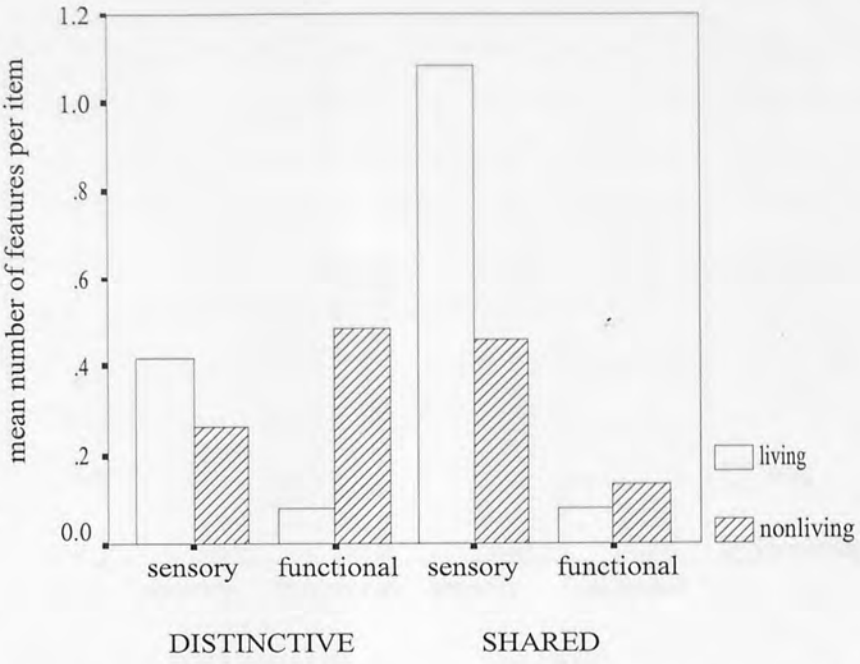


Figure 2.2. The mean number of distinctive and shared features generated for living and nonliving things for the comparison between sensory and functional (narrow) features.

For the sensory-functional (wide) comparison there were more shared than distinctive features, [F (1, 296) = 3.84, p=0.05], and also main effects for feature-type (sensory more than functional) [F (1, 296) = 39.08, p<0.01], and category (living more than nonliving) [F (1, 296) = 4.65, p<0.05]. In addition, an interaction between feature-type and distinctive/shared was found [F (1, 296) = 66.92, p<0.01], i.e., distinctive and shared features differed in terms of their ratio of sensory-functional features, which was greater for the latter (see Table 2.10). There was also an interaction between feature-type and category [F (1, 296) = 49.29, p<0.01], i.e., living and nonliving things differed in terms of their ratio of sensory-functional features, which was greater for the former. A final interaction was found between category and distinctive/shared [F (1, 296) = 35.92, p<0.01], i.e., distinctive and shared features differed in terms of the proportion of features generated for living and nonliving

things; there were more shared features for living compared to nonliving things, and more distinctive features for nonliving compared to living things (see Figure 2.3).

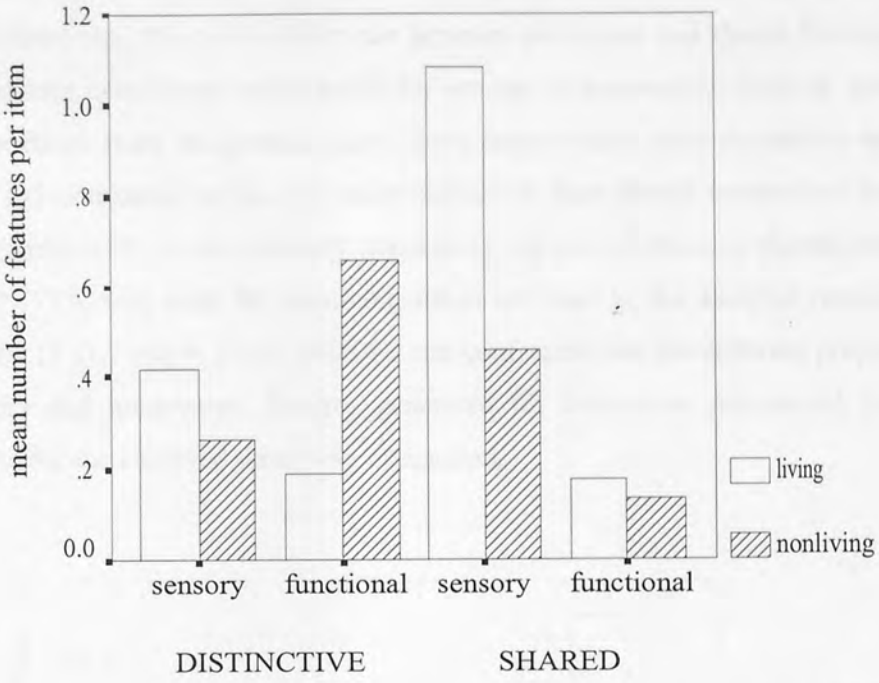


Figure 2.3. The mean number of distinctive and shared features generated for living and nonliving things for the comparison between sensory and functional (wide) features.

Finally, for the sensory-nonsensory comparison there were significantly more shared than distinctive features [$F(1, 296) = 55.62$, $p<0.01$, already observed], in addition to main effects produced for feature-type (nonsensory more sensory) [$F(1, 296) = 32.04$, $p<0.01$], and category (living more than nonliving) [$F(1, 296) = 22.43$, $p<0.01$, already observed]. In addition, an interaction between feature-type and category was found [$F(1, 296) = 9.65$, $p<0.01$], i.e., living and nonliving things differed in terms of their ratio of sensory-nonsensory features (see Table 2.10). There was also an interaction between category and distinctive/shared [$F(1, 296) = 66.09$, $p<0.01$, already observed], i.e., there were more shared features for living compared to nonliving things, and more distinctive features for nonliving compared to living things (see Figure 2.4).

A final three-way interaction was found between distinctive/shared, category, and feature-type [F (1, 296) = 10.88, $p<0.01$], i.e., for living things the difference between distinctive and shared features was significant overall (shared more than distinctive) and of similar proportion individually for sensory and nonsensory features (see Figure 2.4). For nonliving things the difference between distinctive and shared features was not significant overall, nor individually for sensory or nonsensory features, however the proportions were in contrast; there were more shared than distinctive sensory features (35 compared to 20), but more distinctive than shared nonsensory features (71 compared to 51). A two (sensory-nonsensory) by two (distinctive-shared) between items ANOVA with only the nonliving items included in the analysis revealed an interaction [F (1, 150) = 11.26, $p<0.01$], and confirmed that the different proportions of sensory and nonsensory features generated for distinctive and shared features accounted for the observed three-way interaction.

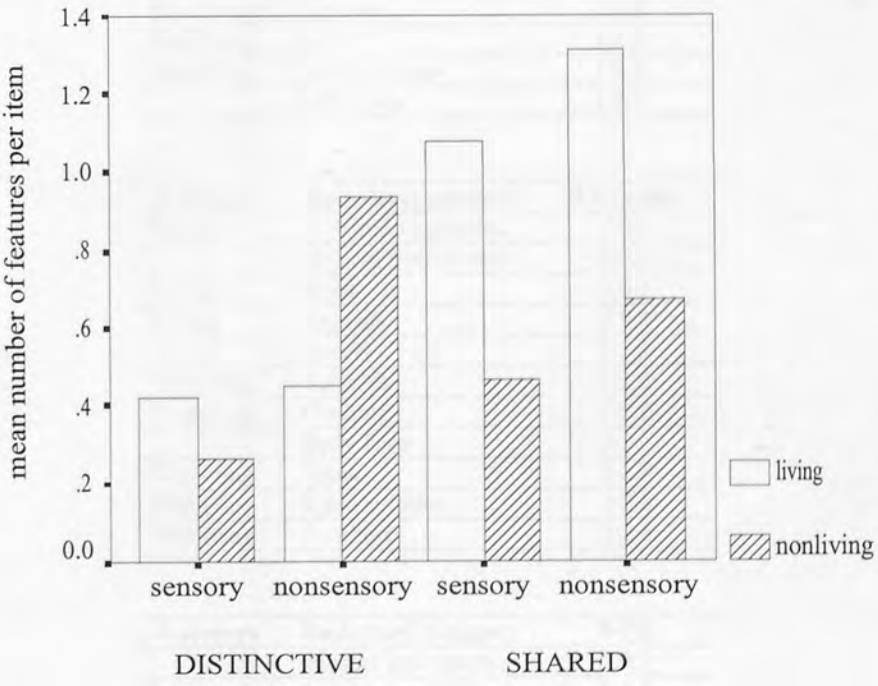


Figure 2.4. The mean number of distinctive and shared features generated for living and nonliving things for the comparison between sensory and nonsensory features.

Basic-level categories

Table 2.11 shows the distribution of distinctive features across all basic-level categories. For the comparison between sensory and functional (narrow) features, the

highest S-F ratio was for fruit and vegetables. Creatures tended to be grouped together with high ratios, whereas nonliving things were grouped together but with much lower ratios. The ratios for musical instruments and body parts were more indicative of living and nonliving things, respectively.

Table 2.11. Basic-level category ratios for distinctive features in descending order for a) sensory-functional (narrow), b) sensory-functional (wide), and c) sensory-nonsensory.

a)

Category	Basic-level category	S-F (narrow)
Living	Fruit and vegetables	7.0:1
	Musical Instruments	6.0:0
Living	Insects	4.0:0
Living	Animals	3.4:1
Living	Birds	3.0:0
Nonliving	Vehicles	2.0:1
Nonliving	Clothing	1:1.7
Nonliving	Furniture	1:1.8
Nonliving	Tools	1:2.2
Nonliving	Kitchen Items	1:2.3
	Body Parts	1:2.7

b)

Category	Basic-level category	S-F (wide)
Living	Fruit and vegetables	7.0:1
	Musical Instruments	6.0:1
Living	Birds	3.0:1
Living	Animals	1.9:1
Living	Insects	1.3:1
Nonliving	Vehicles	1:1.5
Nonliving	Clothing	1:2.0
	Body Parts	1:2.7
Nonliving	Tools	1:2.8
Nonliving	Kitchen Items	1:2.8
Nonliving	Furniture	1:2.8

c)

Category	Basic-level category	S-NS
	Musical Instruments	3.0:1
Living	Fruit and vegetables	1.4:1
Living	Animals	1:1.1
Living	Insects	1:1.1
Living	Birds	1:2.0
Nonliving	Tools	1:2.8
Nonliving	Furniture	1:3.0
Nonliving	Kitchen Items	1:3.0
Nonliving	Vehicles	1:3.5
	Body Parts	1:5.3
Nonliving	Clothing	1:6.7

For the comparison between sensory and functional (wide) the same pattern of results was found, with an even clearer distinction between living and nonliving categories. For the comparison between sensory and nonsensory features, creatures and nonliving things remained grouped together. Musical instruments and fruit and vegetables again had the highest ratios.

Table 2.12 shows the distribution of shared features for basic-level categories. In contrast to the distribution of distinctive features, there did not appear to be any grouping either in terms of living and nonliving things, or the aforementioned creatures, nonliving things, and fruit and vegetable categories. Although the ratios were reduced in size as more functional and nonsensory information was added, a lack of patterning along categorical lines was evident for all three conditions.

Table 2.12. Basic-level category ratios for shared features in descending order for a) sensory-functional (narrow), b) sensory-functional (wide), and c) sensory-nonsensory.

a)

Category	Basic-level category	S-F (narrow)
Living	Fruit and vegetables	15:1
Living	Animals	14:1
Nonliving	Kitchen Items	10:1
	Musical Instruments	8.0:1
Nonliving	Tools	8.0:1
Nonliving	Furniture	6.0:0
Living	Insects	6.0:0
Living	Birds	2.0:1
	Body Parts	2.0:0
Nonliving	Clothing	1.8:1
Nonliving	Vehicles	1:1

b)

Category	Basic-level category	S-F (wide)
Nonliving	Kitchen Items	10:1
	Musical Instruments	8.0:1
Living	Fruit and vegetables	8.0:1
Nonliving	Tools	8.0:1
Living	Animals	7.0:1
Nonliving	Furniture	6.0:0
Living	Insects	6.0:1
	Body Parts	2.0:0
Nonliving	Clothing	1.8:1
Living	Birds	1:1
Nonliving	Vehicles	1:1

c)

Category	Basic-level category	S-NS
Nonliving	Furniture	1.5:1
	Body Parts	1:1
Living	Fruit and vegetables	1:1
Nonliving	Tools	1:1.1
Nonliving	Kitchen Items	1.1:1
	Musical Instruments	1:1.1
Living	Animals	1:1.2
Living	Insects	1:1.3
Nonliving	Vehicles	1:3.0
Nonliving	Clothing	1:3.1
Living	Birds	1:4.0

2.2.7 Discussion

The present results showed that there were more distinctive features associated with nonliving compared to living things overall. McRae and Cree (2002) found the same result using an even larger feature database than that implemented here, as did Garrard et al (2001) and Devlin et al (1998) with their relatively small databases. McRae and Cree argued that the greater number of distinctive features could explain why the majority of patients reported in the literature present with a category-specific impairment for living things, compared to the few with nonliving deficits. Hence, the corresponding finding in the present analysis supported this proposition.

In addition, the present results found that there were significantly more distinctive functional features for nonliving compared to living things (regardless of functional definition), and more distinctive sensory features for living compared to nonliving things (except when all nonsensory features were included). These findings mirrored those in previous sections when all features, and core features were included in the analysis. Therefore, the prediction of the S-F hypothesis that sensory features are critical for distinguishing between living things, and that damage to stored sensory knowledge would result in a category-specific impairment for living things, was substantiated (Warrington & McCarthy, 1987). In contrast to the present findings, Garrard et al (2001) did not find more distinctive sensory features for living compared to nonliving things, but it should be noted that they used a much smaller set of feature norms (30 living and 32 nonliving things).

The present results showed there were significantly more shared sensory features for living compared to nonliving things, but in contrast, the proportion of shared

functional features was similar across category. The exception to this was for the sensory-nonsensory comparison (see right-hand side of Figure 2.4), a finding that was primarily due to the large number of additional shared features classified as superordinate for living compared to nonliving things (62 and 29 respectively, see Table 2.10).

The basic-level category analysis showed a pattern of grouping at a level subordinate to the usual living-nonliving classification, but only for distinctive features. In particular, creatures tended to have similar ratios to each other across each condition, but as with the previous all feature analysis, they appeared to be independent of fruit and vegetables. Similarly, nonliving categories showed comparable ratios to each other throughout and to a greater extent as more features were added. Therefore, although there was some patterning of basic-level categories into distinct groups they tended to remain within their superordinate category. Once again, the exceptions to this were the categories of musical instruments and body parts, which were more indicative of living and nonliving things, respectively.

2.2.8 Feature correlation analysis

In this section, two features were considered correlated if they tended to appear together in the same basic-level items. For example, the features <has feathers> and <has wings> were significantly correlated because living things with feathers (e.g. birds) tended to be described as having wings. Using the feature-norm database, Pearson product moment correlations were calculated between all feature-pairs. Following the method used by McRae and Cree (2002) only those features that appeared in greater than three concepts were included in the correlation analysis. This resulted in 121 different features being included.

Overall, the number of significant correlations found was low. Out of 7708 possible feature combinations 29 (0.38%) were found to be significant at $p<0.05$. Table 2.13 shows the mean number of feature-pair correlations per item across all eleven categories. The category of tools produced the greatest proportion of correlations per item, but this finding was in contrast to the remaining categories, which tended to have a higher number for living than nonliving things. However, the overall greater

proportion of correlations for living compared to nonliving things (mean = 0.22 and 0.12 per item) was not a significant effect [X^2 (1) = 3.51, NS].

Table 2.13. Mean correlations per item across all basic-level categories.

Category	Basic-level category	Mean correlations per item
Nonliving	Tools	0.38
Living	Animals	0.35
Living	Fruit and vegetables	0.27
	Musical Instruments	0.20
Living	Insects	0.13
Living	Birds	0.11
Nonliving	Kitchen Items	0.11
Nonliving	Vehicles	0.08
Nonliving	Clothing	0.05
	Body Parts	0
Nonliving	Furniture	0

Table 2.14 shows the type of features that made up the feature-pair correlations (e.g. for living things the correlated feature-pair <green, round shape> was sensory-sensory). For both living and nonliving things the majority of correlations contained at least one sensory feature (72% and 78% respectively). There were four feature pairs (4/18, 22%) that contained a functional feature for living things (e.g. <is juicy, is eaten>), and four for nonliving things (4/9, 44%) (e.g. <has a blade, used to cut things>). Nonsensory features regularly appeared in correlations for both categories (56% and 44% for living and nonliving things, respectively).

For the type of features that were paired together, both categories had the same proportion of sensory-sensory pairs (33%), and both had two sensory-functional pairs (11% and 22% respectively). Living things had more sensory-nonsensory pairs than nonliving things (39% compared to 22%), and also the only nonsensory-nonsensory correlation, whereas both categories had two functional-nonsensory correlations (11% and 22%).

Table 2.14. Correlated feature-pair types for living and nonliving things

Feature-pair types	Number of correlated pairs		
	Living	Nonliving	Total
Sensory-Nonsensory	7	2	9
Sensory-Sensory	6	3	9
Functional-Nonsensory	2	2	4
Sensory-Functional	2	2	4
Nonsensory-Nonsensory	1	0	1
Total	**18**	**9**	**27**

Distinctive features were not incorporated in the feature correlations analysis because only features that appeared in more than three concepts were included. Hence, shared features were included, and they accounted for the majority of the features involved. Shared features appeared in every nonliving thing correlation (9/9, 100%) and in 14/18 (78%) of correlations for living things. Furthermore, feature correlations containing both shared features (e.g. both features in the correlation <is an animal, has four legs> were shared features) accounted for 8/18 (44%) of living things correlations, and 6/9 (67%) of nonliving things correlations.

2.2.9 Discussion

The greater proportion of significant feature-pair correlations for living compared to nonliving things replicated the results found in previous studies. For instance, McRae et al (1997) also found a nonsignificant difference with more living than nonliving feature correlations. Furthermore, McRae and Cree (2002) found that this nonsignificant pattern changed to a significant finding when their feature-norm database was increased. Garrard et al (2001) found very low mean correlation values for both categories (0.13 and 0.10 for living and nonliving, respectively), but this difference was significant owing to the large number of possible feature pairings.

At the basic category level, with the notable exception of tools, the results from this section indicated that the proportion of feature correlations were similar for living things and also for nonliving things. This finding was in contrast to that of McRae and Cree (2002) who ranked categories in terms of the mean percentage of correlated feature pairs per item and found little evidence of any grouping along categorical lines.

The finding that most feature-pair correlations consisted of shared features was interesting in terms of the number of shared features found overall. The previous section showed that there were significantly more shared features for living compared to nonliving things. Therefore, the fact that more correlated features were found for living things both in this section and in previous studies may result from living things having more shared features than nonliving things, which in turn have more distinctive features that tend not to be as densely correlated.

Therefore, although the numbers of feature correlations were low the results from this section provided some insight into explanations of category-specificity based on feature correlations. As discussed in the introduction to this chapter, the contrasting feature-correlation accounts of category-specificity proposed by Devlin and colleagues (Devlin et al, 1998) and Moss and colleagues (Durrant-Peatfield et al, 1997; Moss et al, 1997, 1998; Tyler & Moss, 1997) both predicted a relationship between severity of damage and category advantage, but they were opposite in direction: For Moss et al, mild damage resulted in an impairment for living things because the strong form-function correlations among the distinctive features of nonliving things were preserved. As damage became more severe the category advantage reversed because shared correlated features provided greater support for living things. For the Devlin et al model, mild damage resulted in an impairment for nonliving things because of the greater number of correlated features for living things overall, but as damage increased there was a more marked decline in identification of living things since these items shared many (damaged) features.

Hence, the present results provided some evidence supporting the Devlin et al model in terms of the (nonsignificant) pattern of more correlated features for living compared to nonliving things, and also for the predictions made by Moss and colleagues by finding that strong correlations existed between the shared features of living things. However, there was little evidence to support the other two model predictions concerning shared features, i.e., only two significant correlations were found between shared sensory and functional features, and none between shared functional features. However, the low numbers of feature correlations found in this section restrict any strong interpretation of either model's predictions.

2.3 GENERAL DISCUSSION

This chapter examined the relationship between feature knowledge and category structure by analysing the feature norms generated by subjects in a semantic definition experiment. When all generated features were considered, those for living things were more numerous than those for nonliving things. Furthermore, the type of features were distributed between the two categories differently: sensory features were more numerous for both categories, but there was a disparity between the numbers of sensory and functional features, i.e., living things tended to be represented by sensory features, and nonliving by functional features. This pattern of results was investigated using all feature-type comparisons previously used in the literature as well as a new method that examined what were termed 'core' features. Regardless of the comparison employed, a distinction was found between the types of features generated for living and nonliving things. Hence, when all feature-types were included in the analysis, the fundamental claim of the S-F hypothesis that semantic knowledge about living and nonliving things is principally encoded in terms of sensory and functional features, respectively, was upheld.

An important aspect of the feature database was that the large number of items allowed those categories subsumed within the living-nonliving classification to be tested in the same way. This analysis showed that three groups - creatures, fruit and vegetables, and nonliving things - tended to group together. This mirrored patient deficits in the literature and also had implications for the domain-specific hypothesis (Caramazza and Shelton, 1998; see Section 1.3.2). Caramazza and Shelton argued against a feature-based explanation of category-specificity and proposed that evolutionary pressures resulted in the development of specialised neural regions for the representation of three different categories: animals, plant life, and artefacts. The present results supported the view of a system differentiated by these three categories, but rather than being the result of damage to specialised neural systems organised by category, impairments for animals, plants, or artefacts could emerge from damage to stored sensory or functional knowledge. Moreover, initial evidence was found for a more distributed model of semantic knowledge (e.g. Warrington & McCarthy, 1987). For instance, different amounts of fine-grained sensory features (e.g. tactile, taste/smell) were generated for different basic-level categories (e.g. fruit, animals). However, the low numbers of features found for these fine-grained categories

restricted any further analysis, and a more detailed feature classification across a much larger set of items would be required to specifically test the distributed model of semantic knowledge.

The core features analysis assessed whether there were a set of features that facilitated item identification more readily, rather than all features contributing equally to an items representation. The overall finding of a distinction between the type of features generated for living and nonliving things remained, however, living and nonliving things were more tightly grouped within their respective categories, and there was more distance between the two categories. Therefore, the core feature analysis revealed that the more frequently a feature was generated, the more likely it was that it would be sensory for living things and functional for nonliving things.

When distinctive features were considered, the findings mirrored those for all features, and core features, providing further evidence that sensory features are critical for distinguishing between living things, and functional features for distinguishing between nonliving things. When shared features were considered, again there were significantly more shared sensory features for living compared to nonliving things, but the proportion of shared functional features was similar across category. Moreover, when the basic-level categories were considered, only distinctive features patterned into living and nonliving categories.

The most striking finding from the distinctive type analysis was that there were significantly more distinctive features associated with nonliving compared to living things. This finding provided an explanation for the disparity in the patient literature between the relatively large number of category-specific impairments for living compared to nonliving things; as previously explained, distinctive features are critical in the identification of items, and therefore, if damage occurred to stored semantic knowledge, a disparity in the proportion of distinctive features associated with living and nonliving things would result in a differential impairment identifying items from the category with less distinctive features, i.e., living things.

When feature correlations were considered, there were more correlations found for living compared to nonliving things, a finding consistent with the model of Devlin et

al. Furthermore, consistent with the predictions of Moss and colleagues, strong correlations between the shared features of living things were found. However, any interpretation of these results must be viewed in light of the relative paucity of feature correlations found, and therefore, the present data provided little insight into explanations of category-specificity based on feature correlations.

In summary, the feature-norm data collected in this chapter revealed a clear distinction between the types of features generated for living and nonliving things, and even for basic-level categories within the living-nonliving classification. For the first time, this was found to be the case when sensory features were compared to functional features for both narrow and wide definitions, and even when sensory features were compared to all nonsensory features. Furthermore, these findings were maintained over three different methods of analyses: 1) all feature-types, 2) core feature-types, and 3) distinctive and shared feature-types. Accordingly, these data revealed that there was a consistent category structure in terms of feature knowledge, and supported the fundamental claim of the S-F hypothesis that semantic knowledge about living and nonliving things is principally encoded in terms of sensory and functional features.

The importance of correlations between features was less clear due to the relatively small number of correlations (see also McRae et al, 1997). However, overall, the data in this chapter demonstrate the value of feature-norm studies as a tool to investigate category-specific deficits. The research has contributed to the literature by increasing the number of items used compared to many studies, and the data indicate that analysis of the features can lead to a more detailed understanding of the factors underlying category-specific semantic deficits.

CHAPTER 3
THE EFFECTS OF TIME ON STORED SEMANTIC KNOWLEDGE: A SINGLE CASE STUDY

3.1 INTRODUCTION

In this chapter a 12-year longitudinal case study on a 60 year-old male patient (DW) with category-specific agnosia is reported. Agnosia is an impairment characterised by an inability to recognise familiar objects in one or more sensory modalities. Visual agnosia is by far the most common form and has been documented in the literature for over a century (e.g. Lissauer, 1890). Lissauer distinguished between two different forms of agnosia: apperceptive and associative. Apperceptive refers to a recognition deficit that is due to disrupted perceptual processing in patients with relatively intact elementary sensory functions (such as visual acuity and movement perception). In contrast, associative agnosic patients have intact perceptual processing but access to stored semantic knowledge necessary for recognition is disrupted. Since Lissauer's description of these phenomena, there have been numerous reports of visual agnosia. These have provided invaluable insights into the organisation and anatomy of normal visual recognition.

However, the vast majority of these studies have been conducted over a relatively short time period when the patients' abilities and impairments remained stable and only four studies have specifically investigated how the pattern of visual agnosia can change over a longer period of time (Kertesz, 1979; Riddoch et al, 1999; Sparr et al, 1991; Wilson & Davidoff, 1993). These longitudinal studies are particularly interesting because whether an impairment changes or remains stable may provide clues about the underlying nature of the disorder and the organisation of brain function. For example, improvements in a patient's performance may inform us about the extent of brain plasticity and/or about the compensatory strategies that can be used to help patients learn new ways to accomplish particular tasks. In contrast, further degradation in patient's performance over time may highlight the cognitive abilities that require 'up-dating' or maintenance from information that is no longer available.

As background to the current case study, the main features of the four longitudinal studies of visual agnosia are briefly summarised. Sparr et al (1991) described a 40-

year follow-up study on a 62-year-old female patient (HC) first examined by Adler (1944, 1950). HC suffered anoxic damage resulting in bilateral occipital atrophy. Adler initially reported that HC presented with apperceptive visual agnosia for faces (prosopagnosia) and objects. Six months post-injury her deficit had improved to the extent that under normal viewing conditions only her prosopagnosia remained, although she still had difficulty recognising pictures when they were presented briefly. In the follow-up report, Sparr et al (1991) noted that while HC had no difficulty with object recognition under normal viewing conditions her problems under constrained visual conditions had persisted over time (i.e. a finding commensurate with Adler's some 40 years earlier). Therefore, HC showed no recovery or further deterioration of function after the initial six-month period.

Wilson and Davidoff (1993) presented a follow-up study on a 29-year-old female patient (JR) who presented with visual and tactile agnosia when she was examined 10 years earlier (Davidoff & Wilson, 1985). JR sustained a head-injury resulting in marked dilation of the ventricular system particularly worse on the left occipital horn extending to the occipital lobe. She initially presented with impairment in the visual recognition of real objects, photographs and line drawings. Over a period of seven months post-injury, however, she showed some recovery of function. Her visual recognition of real objects improved from 25% to 38% correct, object recognition for photographs from conventional views improved from 5% to 35% correct, and recognition of line drawings improved from 3% to 10% correct. Davidoff and Wilson repeatedly assessed JR over the ten-year period and observed a continual improvement in her performance. At the time of her final assessment in 1992, her visual recognition of real objects had improved to 100% correct, photographs to 82% correct, and line drawings to 53% correct (Wilson & Davidoff, 1993). Additionally, when first tested, JR was unable to recognise any real objects from palpation alone; seven years post-injury JR had improved significantly with all objects correctly identified using the left and right hands. In contrast to patient HC, therefore, JR exhibited a significant, consistent recovery of function over a ten-year period of assessment.

Kertesz (1979) conducted a nine-year follow-up study on a 41-year-old female patient who suffered a head injury resulting in visual agnosia. A CT scan showed decreased

absorption from the right frontal horn of the lateral ventricle and in the left occipital lobe, and an electroencephalogram (EEG) showed irregular theta activity in the right parietal lobe. The patient's recognition of real objects improved slightly over the nine-year period from 35% to 45% correct. However, her recognition of line drawings remained constant (10% and 9% correct, respectively).

Riddoch et al (1999) reported a follow-up study on a 77-year-old male patient (HJA) with visual agnosia, first examined by the same authors 10 years earlier (Riddoch & Humphreys, 1987). This case is discussed in detail throughout this chapter because HJA is similar to DW, the patient investigated here. HJA suffered a posterior cerebral artery stroke in 1981, resulting in bilateral lesions of the occipital lobe, extending anteriorly towards the temporal lobes. His perceptual processing abilities have remained stable over time. In both 1987 and 1997 he was able to copy visually presented line drawings, suggesting that some aspects of his perception of object form were intact. The authors noted, however, that he adopted a slow, part-by-part method of copying. In an overlapping figures test, which requires the subject to identify letters superimposed over each other, HJA had significant difficulties compared to age-matched controls, suggesting that he had problems when visual stimuli had to be segregated. Again, this impairment was stable over time. In tests of object recognition, HJA showed an improvement over time for real objects, increasing from 28/45 (62%) correct in 1987 to 34/39 (87%) correct in 1997. In contrast, his recognition of line drawings showed no significant improvement, scoring 36/75 (48%) correct and 41/76 (54%) correct for 1987 and 1997, respectively.

Visual agnosic patients tend to be better at identifying real objects compared to line drawings and a number of authors (e.g. Chainey & Humphreys, 2001) have suggested that this may be because additional properties of real objects (e.g. depth cues, surface texture, and colour), not available in line drawings, facilitate patients' recognition. Moreover, patients may be able to examine real objects from many viewpoints rather than the one static orientation available in line drawings, thereby increasing access to stored structural descriptions. In this chapter, longitudinal data from patient DW is presented who had a similar visual agnosia to HJA. It was found that DW also showed a significant improvement in his ability to recognise real objects. The factors that facilitated his performance over time are investigated.

Riddoch et al (1999) also reported that HJA's ability to draw objects from memory and to recall the visual features of objects in a verbal definitions task had significantly deteriorated over time. This is interesting because HJA's increased difficulty in accessing stored visual knowledge at time 2 suggests that visual knowledge deteriorates over time unless it is 'updated' by visual perception. Indeed, these findings led the authors to conclude that visual perception and stored knowledge of visual features are not functionally independent but have important interactive links. This contrasts with others (e.g. Behrmann et al, 1992) who propose that the perceptual and memorial processes involved in object recognition are functionally independent. According to this hypothesis, poor visual perception should have no knock-on effects on stored visual knowledge. In this chapter, the extent to which visual experience is required to maintain stored knowledge about the visual attributes of objects is investigated by assessing whether DW's stored visual knowledge has deteriorated or remained stable over time.

One further interesting feature of HJA's object recognition was an apparent category-specific effect (Riddoch and Humphreys, 1987). In particular, HJA found it more difficult to identify living things compared to nonliving things. There has been a relatively large number of category-specific cases documented in the neuropsychological literature (see Section 1.2). Riddoch et al (1999) assessed the effects of time on HJA's ability to recognise objects from different categories and found that the deficit for living things remained over the 10-year period. In addition, when HJA was asked to provide definitions of objects a differential effect for the category of living objects compared to nonliving objects was observed. In particular, his ability to generate the visual features of objects had deteriorated more for living than for nonliving things. Note that there was not a general decrease in stored information over time: HJA's ability to recall nonvisual features was equally good for the living and nonliving things. This chapter reports that patient DW also has a category-specific impairment for living things. In Section 3.3 the impact of this impairment on his ability to retrieve the visual features of objects from each category is assessed. The implications of these data for theories of category-specific impairments and for the links between on-line visual perception and stored visual knowledge are discussed in Section 3.4.

3.2 CASE REPORT

DW was 61 years old at the beginning of the present investigations (01-02-00). A right-handed man, he has suffered from epilepsy since the age of 20. During his working life he trained as an electronic engineer and was working as an electronic tester when, in July 1985, he sustained a head injury. He had an epileptic fit whilst climbing a ladder, lost consciousness, and fell backwards hitting his head. The fall resulted in a linear occipital fracture to the skull and internal damage to the right frontal lobe and bilateral occipital lobes. A CT scan revealed bilateral intracerebral frontal contusions, particularly on the right. Two days after admission to hospital, DW again lost consciousness. A right frontal craniotomy and right frontal lobectomy was considered necessary to relieve the pressure within the brain. A CT scan conducted in March 1987 (20 months post-onset) revealed residual bilateral occipital and frontal lobe damage. When DW recovered from surgery, he initially presented with cortical blindness. However, over a two-year period his sight gradually improved, although examination of his visual fields revealed a complete left homonymous hemianopia and a right field acuity restriction. However, DW's vision was sufficient for him to orient himself, read and watch television.

DW's orientation in time and place was good as assessed by the Wechsler Memory Scale test (Wechsler, 1997). His short-term memory span was within the normal range: digit span was 5 forwards and 4 backwards. He had some difficulty reading words although no effect of regularity was found: he scored 26/30 and 27/30 for regular and exception words on PALPA Test 35 (Kay et al, 1973). He was also able to access the meaning of words and scored within control range on the word version of the Pyramid and Palm Trees test (49/52 correct). On the picture version of this test, he scored only 29/52 correct (Howard & Patterson, 1992).

3.2.1 Visual perceptual processing ability

A number of tests from the Birmingham Object Recognition Battery (BORB) (Riddoch & Humphreys, 1993) were carried out to assess DW's low-level perceptual abilities (matching of line lengths and orientations, and matching shapes for size). In general, he scored within the normal control ranges (see Table 3.1). This indicates that his inability to name objects (see Experiment 1 below) was not simply because he could not detect the size of the shapes or the orientation of the lines.

Table 3.1. BORB tests of low-level vision.

BORB tests	DW	Control Range
Test 2 (Length Matching)	25/30 (83.3%)	22-30
Test 3 (Orientation Matching)	23/30 (76.7%)	18-29
Test 4 (Orientation Matching)	23/30 (76.7%)	18-29
Test 7 (Minimal Feature View)	18/25 (72%)	18.5-25
Test 8 (Foreshortened View)	18/25 (72%)	16.7-25

DW's ability to separate figure from ground was assessed by superimposing one drawing onto another and asking him to draw around the outline of one of the two pictures. The two pictures were from the same superordinate category. Successful completion of this task requires the ability to group the different parts of one object together while concurrently ignoring the parts of the other. DW had considerable difficulty with this task and was only able to correctly outline 14/37 (38%) of the items. DW's ability to separate figure from ground was compared with control data by carrying out a second overlapping figures test (BORB Test 6). In this task DW was asked to name sets of letters and sets of geometric shapes. Both stimuli sets were organised in five ways; single, paired non-overlapping, paired overlapping, triplets non-overlapping, and triplets overlapping. Performance was timed, and the difference between naming of stimuli in overlapping and non-overlapping conditions was expressed as a ratio. Compared to control subjects DW was impaired in all conditions (see Table 3.2).

Table 3.2. Ratio of naming overlapping and non-overlapping stimuli

Condition	DW	Control Mean
Letters paired	1.0:1.4	1.0:1.2
Letters triplets	1.0:1.4	1.0:1.1
Shapes paired	1.0:1.2	1.0:1.0
Shapes triplets	1.0:1.5	1.0:1.1

DW was requested to copy 9 line drawings (4 living items and 5 nonliving items), one at a time. His copying was a laborious, piecemeal process and he tended to concentrate on one feature at a time. For example, in copying a picture of a horse (see Figure 3.1) he drew the front legs first, followed by the back legs, then the head and,

consequently, although each part was competently copied, difficulties emerged when he attempted to join up the parts as a whole.

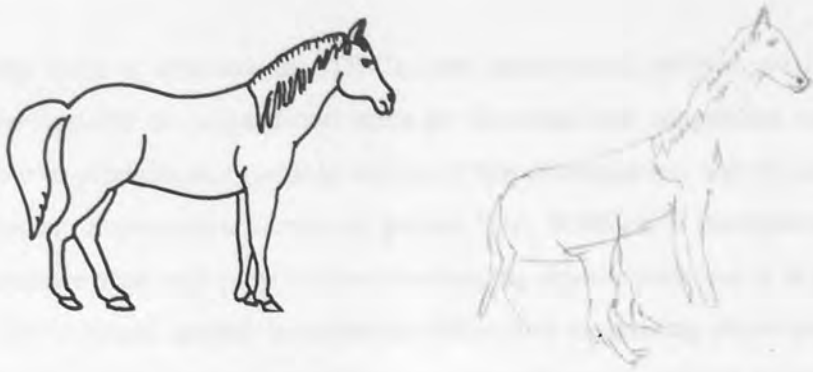


Figure 3.1. An original line drawing taken from the Birmingham Object Recognition Battery (Test 14) with DW's corresponding copy on the right.

DW's performance on tests of object constancy was also assessed, i.e., his ability to judge that an object remains the same when viewed from different positions. He performed both the foreshortened view and the minimal-feature view matching tests taken from BORB (tests 7 and 8). These involve the presentation of three pictures per trial. One picture shows the object from a standard viewpoint, another picture shows the same object from an unusual view, and a third shows a different object. DW was required to indicate whether the second or third picture matched the first. In the minimal features task, the unusual view picture was rotated to obscure the main identifying feature of the object, and in the foreshortened view task, it was rotated in depth to change the relationship between the object's main axis and its parts. DW scored 18/25 (72%) correct on the foreshortened view task, which was within the control range [control mean = 21.6/25, range = 16.7-25, *SD* = 2.6], but on the minimal-feature view task he scored 18/25 (72%) correct, which was just outside control range [control mean = 23.3/25, range = 18.5-25, *SD* = 2.0]. In 1988, DW also performed at a normal level on a foreshortened views test (30/32, 94%) with photographs, and slightly worse on minimal features views (28/32, 88%). This pattern of poorer performance on the minimal features task compared to the foreshortened view task is relatively unusual (Riddoch & Humphreys, 1993). It suggests that DW may be using local features to identify objects - minimal features views then become

difficult because these features are obscured. Objects in foreshortened views can still be identified because the features remain visible (see Humphreys & Riddoch, 1984, for further discussion of these tasks).

In summary, there is evidence that DW's most basic visual abilities are intact. For instance, he was able to judge if two items are the same size, length and orientation. He was able to produce recognisable copies of line drawings but only by adopting a slavish, piecemeal procedure (similar to patient HJA, Riddoch & Humphreys, 1987). His performance was very poor on two overlapping figures tests and it is suggested here that DW's visual agnosia is related to difficulties integrating object parts into a coherent whole. DW's pattern of abilities and impairments is similar to patient HJA and it is concluded that DW can also be classified as an 'integrative agnosic'.

3.3 EXPERIMENTAL INVESTIGATIONS

3.3.1 Naming Living and Nonliving Things

Experiment 1. Picture Naming

Method

DW was presented with 76 line drawings (BORB Test 13) in 1988 and 2000. Pictures were presented one at a time and DW was asked to name them. No time constraints were set. Half the items were pictures of living things and half were pictures of nonliving things. Within the living and nonliving categories, half the items had high name frequencies and half had low name frequencies. Pictures were pairwise matched on this basis (see Kucera & Francis, 1967 for name frequency norms).

Results

There was no significant difference in DW's naming performance between 1988 (28/76, 36.8%) and 2000 (23/76, 30.3%) [X^2 (1) <1]. In 1988 he was significantly impaired at naming living items (4/38, 10.5%) in comparison to nonliving items (24/38, 63.2%) [X^2 (1) = 22.62, $p<0.01$]. In 2000 he was also significantly impaired at naming living items (2/38, 5.3%) in comparison to nonliving items (21/38, 55.3%) [X^2 (1) = 20.53, $p<0.01$]. There was a high degree of consistency of response between the two assessments, with 86.8% of the living items [C = 0.57, $p<0.01$] and 71.1% of the nonliving items [C = 0.46, $p<0.01$] either consistently correct or incorrect over time. DW's error types are shown in Table 3.3. In both 1988 and 2000 he made more

superordinate errors (e.g. he named a bear as 'an animal' and a lemon as 'a fruit') when attempting to name living items than he did for nonliving items. Also for living things, there were more semantic errors (e.g. he named a tiger as 'a donkey') and visual-semantic errors (e.g. he named a squirrel as 'a cat'), whereas, for nonliving things visual errors were more common (e.g. he named an ashtray as a 'mirror with hole'). This error pattern suggests that DW can sometimes recognise the superordinate category of a living thing but is unable to distinguish between the target and related exemplars.

To control for confounding variables, such as familiarity, visual complexity and name frequency, DW's naming accuracy data for was entered into a logistic regression analysis with four independent variables: 1) category (living/nonliving), 2) name frequency, 3) visual complexity and 4) familiarity. In 2000 the variables; category (Wald = 8.18, $p<0.01$) and name frequency (Wald = 5.36, $p<0.05$) had a significant effect on DW's picture naming accuracy, whereas the variables; familiarity (Wald = 0.01, NS) and complexity (Wald = 2.38, NS) did not. In 1988 the variable; category (Wald = 9.76, $p<0.01$) had a significant effect on naming performance, whereas the variables; name frequency (Wald = 0.35, NS), complexity (Wald = 1.34, NS), and familiarity (Wald = 0.92, NS) did not. Therefore, the category effect was found to be highly significant and accounted for the majority of the variance observed in DW's naming performance at both time 1 and time 2.

Table 3.3. DW's error types in naming.

	1988		2000	
Error Type	Living	Nonliving	Living	Nonliving
Visual	1 (3)	6 (40)	2 (6)	7 (41)
Semantic	6 (17)	1 (7)	6 (17)	0
Visual-semantic	5 (14)	1 (7)	8 (22)	3 (18)
Superordinate	11 (31)	1 (7)	12 (33)	0
Don't know	12 (34)	6 (40)	8 (22)	7 (41)
Total	35	15	36	17

Table 3.4. DW's naming of living and nonliving things.

	1988		2000	
Naming	Living	Nonliving	Living	Nonliving
Line Drawings	4/38	24/38	2/38	21/38
Real Objects (vision)	7/28	24/45	5/28	37/45
Real Objects (touch)	--	13/21	--	14/21
Real Objects (taste)	1/9	--	2/9	--
Definitions (perceptual)	11/38	21/38	11/38	17/38
Definitions (functional)	35/38	38/38	28/38	35/38

Experiment 2. Real Object Naming

Method

In 1988 and 2000 DW was presented with 73 real objects and requested to name them from vision alone. Twenty-eight were living objects (fruit and vegetables) and 45 were nonliving objects (e.g. tools and household items). The objects were randomly presented, one at a time, on a table approximately 500cm away from DW. He was not permitted to touch or have the presented object moved. No time constraints were set.

Results

In 1988, DW was significantly impaired at naming living objects (7/28, 25%) compared to nonliving objects (24/45, 53.3%) [X^2 (1) = 5.67, $p<0.05$]. In 2000 he was also significantly impaired at naming living objects (5/28, 17.9%) compared to nonliving objects (37/45, 82.2%) [X^2 (1) = 36.04, $p<0.01$]. Although the observed pattern of a category-specific impairment for living objects remained across both assessments (see Table 3.4), DW's ability to name nonliving objects had significantly improved over time [X^2 (1) = 9.36, $p<0.01$]. His difficulties in naming living objects remained at a stable level [X^2 (1) = <1]. Additionally, there was a high degree of consistency of response between the two assessments [89.3% for living things, C = 0.55, $p<0.01$; and 66.7% for nonliving things, C = 0.36, $p<0.05$].

Discussion

In data collected for the present report, DW's naming of line drawings and real objects was significantly impaired for the category of living things compared to nonliving things. This pattern was consistent over the 12-year period. He showed no significant improvement over time, except for his ability to name real nonliving

objects from vision. His ability to name real living things (i.e. fruit and vegetables) and pictures of both categories did not improve. What could explain his improvement for recognising real nonliving objects? One explanation is that, over time, visual processing has improved, resulting in an ability to recognise objects that had previously been difficult. Alternatively, over time DW may have learned to use compensatory strategies to help him identify objects. If his visual recognition abilities had recovered, a general pattern of improvement over time on tests that tapped similar abilities would be expected, for example, an improvement in naming line drawings and in naming real objects from all categories. This was not the case, however, suggesting that his improvement with real objects was due to more efficient use of compensatory strategies. It is noted that an improvement in recognising real objects but not line drawings was also reported in two other longitudinal studies (Kertesz, 1979; Riddoch et al, 1999). As alluded to in Section 3.1, this may be due to better use of properties such as depth, texture, and colour information and/or the incremental effects of multiple object orientations enabling better access to stored structural descriptions. The factors that led to DW's real nonliving object improvement were examined in the following experiments.

3.3.2 A Nonliving Object Improvement Over Time

Experiment 3. Effects of colour and texture on picture naming

Price and Humphreys (1989) found that normal subjects identified coloured line drawings faster than black-and-white line drawings, particularly if colour was consistently linked with the object (e.g. particularly for living things rather than nonliving things). Furthermore, the authors found that normal subjects identified objects with appropriate texture and shading (e.g. photographs) faster than line drawings. In the following experiment Price and Humphreys's (1989) stimuli are used to assess the role of colour and texture in DW's recognition of objects. It was examined whether DW was better at identifying coloured line drawings compared to black-and-white line drawings, and also coloured photographs compared to black-and-white photographs. In addition, the role of texture and shading was investigated by examining whether he was better at identifying black-and-white photographs than black-and-white line drawings.

Method

DW was presented with five sets of stimuli: (1) coloured photographs, (2) black-and-white photographs, (3) correctly coloured line drawings, (4) incorrectly coloured line drawings, (5) black-and-white line drawings. Contained within each set were the same 89 items (42 living, 30 nonliving, 17 others (food items and body parts)). Pictures were presented one at a time and DW was asked to name them. No time constraints were set. Each one of the five sets was presented at a separate experimental testing session.

Results

The results are shown in Table 3.5. Again, DW was consistently better at naming nonliving compared to living things. There was, however, no significant difference between any of the experimental conditions [X^2 (4) = <1]. Indeed, there was a high degree of consistency of response between the five conditions, with 92.1% of all items [C = 0.58, p<0.01] either consistently correct or incorrect.

Table 3.5. DW's naming of black and white and coloured stimuli.

	Living	Nonliving	Others	Total
Black-and-white drawings	4/42 (9.5%)	12/30 (40%)	2/17 (11.8%)	18/89 (20.2%)
Correct colour drawings	5/42 (11.9%)	10/30 (33.3%)	3/17 (17.6%)	18/89 (20.2%)
Incorrect colour drawings	4/42 (9.5%)	12/30 (40%)	3/17 (17.6%)	19/89 (21.3%)
Black-and-white photographs	7/42 (16.7%)	10/30 (33.3%)	4/17 (23.5%)	21/89 (23.6%)
Colour photographs	7/42 (16.7%)	10/30 (33.3%)	3/17 (17.6%)	20/89 (22.5%)

Discussion

This experiment further confirmed DW's poor object recognition ability. However, unlike controls (see Price & Humphreys, 1989), DW showed no effect of colour or texture/shading. This indicates that the improvement in DW's naming of real objects over time was not due to an increased use of these visual cues. In the next experiment it was assessed whether DW might be using depth cues available in real objects but not line drawings to improve his object recognition.

Experiment 4. Effects of depth on real object naming

Chainay and Humphreys (2001) examined how depth information affected patient HJA's identification of real objects. They found that HJA was better at recognising real objects compared to line drawings over a number of conditions except when viewing real objects was controlled so that objects were presented further than arm's reach away (150cm) and with a fixed head position. HJA's recognition was, however, better with objects when they were either close (even when his head was in a fixed position) or when he was able to make head movements (even when objects were distant). The combination of eliminating the opportunity for head movements and placing objects at a distance appeared to impair HJA's recognition by removing two depth cues normally available when identifying real objects. First, stereo disparity, which is reduced as the distance between subject and object is increased (Julesz, 1971). Second, motion parallax, which is removed by restricting lateral head movements (Larson & Simonet, 1992). In the following experiment it was assessed if DW's ability to recognise real objects was also affected by these depth cues.

Method

DW was presented with 42 real nonliving objects on four separate occasions, in four different experimental conditions: (1) Free close; objects viewed at a distance of 45cm with free lateral head movements and full binocular vision. Here both stereo disparity and motion parallax are available. (2) Free distant; objects viewed at a distance of 150cm with free lateral head movements and full binocular vision. Here stereo disparity is removed and motion parallax is available. (3) Fixed close; objects viewed at a distance of 45cm with restricted lateral head movement and full binocular vision. Here stereo disparity is available and motion parallax is restricted. (4) Fixed distant; objects viewed at a distance of 150cm with restricted lateral head movements and full binocular vision. Here both stereo disparity and motion parallax is restricted. Objects were presented one at a time and DW was asked to name them. No time constraints were set.

Results

The results are illustrated in Figure 3.2 and clearly show an effect of viewing condition [X^2 (3) = 14.25, $p<0.01$]. There was no significant difference between DW's performance on the free close, free distant, and fixed close conditions [X^2 (1),

all <1]. In the fixed distant condition, however, his performance differed significantly from all other conditions [X^2 (1), all $p<0.01$].

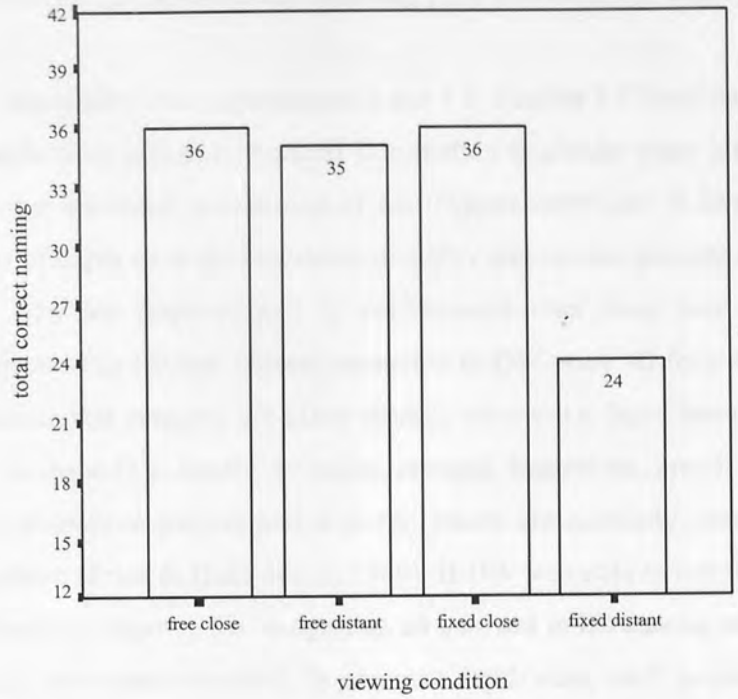


Figure 3.2. DW's correctly identified real objects in four different viewing conditions.

Discussion

The findings from this experiment demonstrate that, when DW could rely on cues from either motion parallax (in the head free conditions) or stereo disparity (in the distant conditions), his object recognition remained relatively good. However, when depth cues from stereo disparity and motion parallax were both reduced, DW's ability to identify real nonliving objects declined (see Chainey & Humphreys, 2001, for a similar finding in patient HJA). It is proposed, therefore, that DW normally uses both stereo disparity and motion parallax to help him recognise real objects, leading to the suggestion that, compared to when he was tested in 1988, he has learnt to use these cues to facilitate his object recognition. It is suggested here that lateral head movements allow for multiple views of 3-D objects that produce a range of related orientations. This may benefit DW's recognition by enhancing the quantity and quality of visual input, and increasing the probability of effectively matching one or more orientation to stored visual knowledge. Chainay and Humphreys (2001) argued

that depth cues provide additional information that facilitates the encoding of relationships between surfaces and parts of objects. This would benefit DW's object recognition because, as was demonstrated in tests of copying and in both overlapping figures experiments, he had difficulty encoding parts into coherent whole objects.

In summary, the results from experiments 3 and 4 in Section 3.3 have shown that DW does not benefit from colour or textural information available when identifying real objects, and that his better recognition of real objects compared to line drawings is due to his use of depth cues such as stereo disparity and motion parallax. Perhaps this can explain why his improvement in performance over time was restricted to nonliving objects. The 'living' objects presented to DW were all fruit or vegetables. Exemplars within this category are often visually simple (i.e. have few parts) and are symmetrical in shape (e.g. apples, tomatoes, oranges, lemons etc, are all round). They tend to have distinctive colours and textures, which are normally used to facilitate object recognition (Price & Humphreys, 1989). If DW was able to use the colour and texture of objects to improve his recognition an increase in his naming of living items over time may have been expected. In contrast, depth cues, such as stereo disparity and motion parallax are more likely to facilitate the recognition of nonliving objects because these objects tend to have several surfaces formed by the relations between their parts.

3.3.3 Access to Stored Visual Knowledge

The experimental data presented thus far has shown that DW has a category-specific impairment for living compared to nonliving things that has remained consistent over a 12-year period. It was also demonstrated that DW was better at recognising real objects compared to line drawings and that his ability to name real nonliving things improved over time. It was shown that DW's use of depth cues was an influential factor underlying this improvement in naming real objects. In this section, whether DW's visual recognition problems have affected his ability to access stored visual knowledge is evaluated by testing his: drawing from memory (Experiment 5); generation of visual and semantic features associated with objects (Experiment 6); naming of items from definitions that stressed the visual and functional features of objects (Experiment 7); accessing information about the size (Experiment 8) and the colour of objects (Experiment 9). The data will be examined to assess if stored visual

knowledge requires maintenance or 'up-dating' from visual perception or if these processes are functionally separable. The former hypothesis predicts that DW's visual knowledge should decline (since he has an impairment to on-line visual recognition) (Riddoch et al, 1999). The latter predicts that an impairment in visual perception should have no knock-on effects for stored visual knowledge (Behrmann et al, 1992).

Experiment 5. Drawing from Memory

Method

DW was requested to draw 35 items from memory (18 living, 17 nonliving) in a random order in a booklet of A4 paper sheets at both t1 (1988) and t2 (2000). No time constraints were set. Two age-matched control subjects (aged 58 and 60) were asked to draw the same 35 items under the same conditions as DW. The drawings were subsequently analysed by asking twelve independent subjects to identify each drawing. Each subject was presented with the items in a different random order. They were informed that the same item could appear in the set a number of times. No time constraints were set.

Results

Figure 3.3 illustrates two representative examples of DW's drawings from memory. Figure 3.4 illustrates the proportion of drawings that were correctly identified by subjects for DW at both time 1 (1988) and time 2 (2000) and for the age-matched control subjects. The identification scores for DW's drawings (i.e. the proportion of subjects who correctly identified a picture) were analysed using a two-way mixed design ANOVA with factors, Category (living, nonliving) and Time (1988, 2000). Significant main effects were observed for both Category [$F(1, 22) = 458.03$, $p<0.01$] and Time [$F(1, 22) = 56.86$, $p<0.01$]. No significant interaction between Time and Category was observed [$F(1, 22) = 1.68$, NS].

a) Aeroplane b) Bear

Figure 3.3. DW's drawing from memory

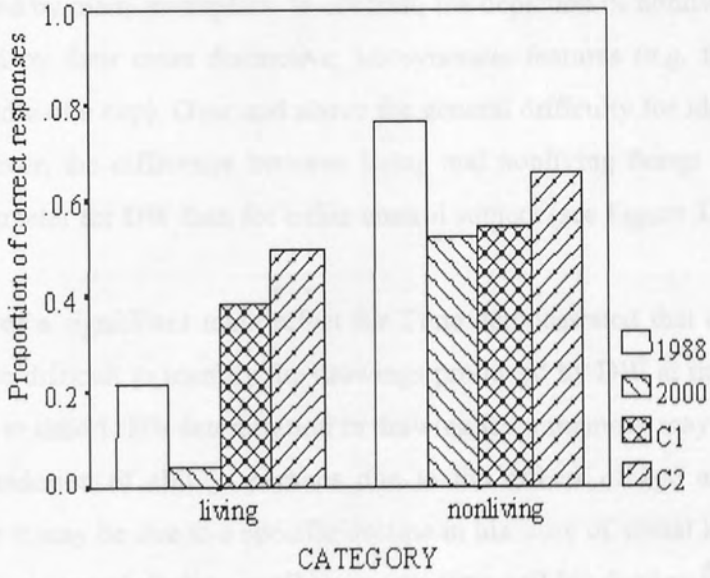


Figure 3.4. DW's (time 1 and time 2) and both control subjects' correctly identified drawings from memory.

Two separate mixed design ANOVAs were carried out comparing the proportion of correctly identified drawings of both control subjects and DW at t1, and both control subjects and DW at t2. The within-stimulus factor was Subject (DW, C1, C2) and the between-stimulus factor was Category (living, nonliving). A significant main effect for Subject was observed at both t1 [$F(2, 44) = 12.21$, $p<0.01$] and t2 [$F(2, 44) =$

128.48, $p<0.01$]. A significant main effect for Category was observed at both t1 [$F(1, 22) = 155.45$, $p<0.01$] and t2 [$F(1, 22) = 239.36$, $p<0.01$]. A significant interaction between Subject and Category was observed at both t1 [$F(2, 44) = 61.48$, $p<0.01$] and t2 [$F(2, 44) = 49.20$, $p<0.01$].

Discussion

It is evident from the analysis of each subject's set of drawings that living objects are more difficult to depict than nonliving things, at least in terms of subjects' ability to identify the drawings in a subsequent task. This may be because living objects are more structurally similar to each other than nonliving objects (Humphreys et al, 1988), and, as a consequence, exemplars from this category are more difficult to draw because subjects must depict subtle changes in the overall shape and size of features that are shared by many exemplars. In contrast, the depiction of nonliving objects can be facilitated by their more distinctive, idiosyncratic features (e.g. the prongs of a fork, the handle of a cup). Over and above the general difficulty for identifying living things, however, the difference between living and nonliving things was more than three times greater for DW than for either control subject (see Figure 3.4).

The finding of a significant main effect for Time demonstrated that control subjects found it more difficult to identify the drawings produced by DW at time 2 than those he produced at time 1. His deterioration in drawing from memory may be the result of general degradation of ability, perhaps due to the effects of age and/or cognitive inactivity, or it may be due to a specific decline in his store of visual knowledge. DW did not show a general decline in all tests over time and his decline in drawing from memory is unlikely to be a consequence of poor visuomotor skills because there was no notable change in his copies of line drawings. Therefore, it is proposed here that DW's stored visual knowledge has deteriorated, and moreover, that this degradation may be the result of a perceptual processing impairment that has failed to maintain or update DW's store of visual knowledge. This issue is discussed in more detail in Section 3.4.

Experiment 6. Verbal Definitions

Method

In 1988 and 2000 DW was requested to produce 43 verbal definitions to verbally presented object names (23 living items and 20 nonliving items). His performance at both time 1 and time 2 was assessed by a set of 12 independent subjects who were asked to identify each of his definitions. The 12 subjects were presented with a booklet containing all 86 definitions and asked to identify each one; each booklet contained the definitions in a different randomly assigned order. In addition, the features he generated were classified according to the following system:

(1) Visual Features

(2) Non-perceptual Features:

a) Functional (an objects use, e.g. kettle – boiling water)

b) Associated action (an action associated with the object, e.g. hammer - strike things)

(3) Superordinate (e.g. cat – animal)

(4) Others

Results

The identification scores (i.e. the proportion of subjects who correctly identified a definition) were analysed using a two-way mixed design ANOVA with factors, Category (living, nonliving) and Time (1988, 2000). Significant main effects were found for both Category [$F(1, 22) = 112.72$, $p<0.01$] and Time [$F(1, 22) = 245.70$, $p<0.01$]. No significant interaction between Time and Category was found [$F(1, 22) = 0.58$, NS] (see Figure 3.6). Subjects found it more difficult to identify living objects than nonliving from DW's definitions at both t1 and t2. However, the proportion of correctly identified definitions for both categories showed a pattern of improvement over time. Living object identification increased from 45% to 75%, and nonliving object identification increased from 65% to 90%.

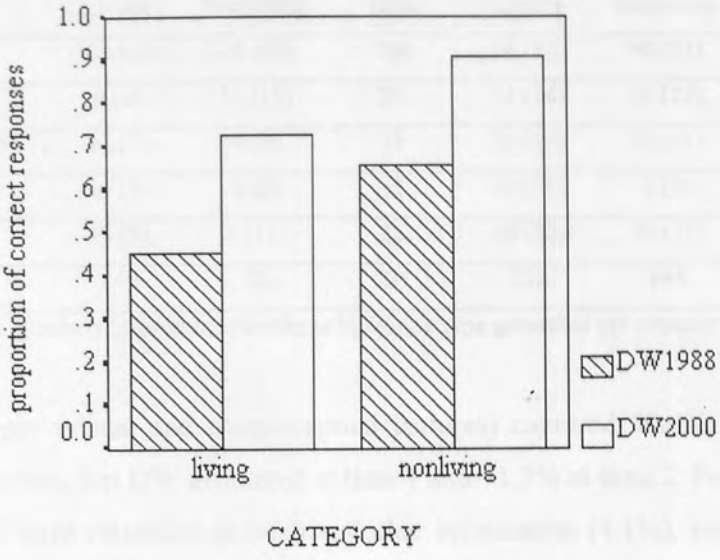


Figure 3.5. DW's correctly identified verbal definitions at both time 1 and time 2.

Total and type of generated features

DW generated a total of 221 features for the 43 items at time 1 (mean 5.1 features per item) and 362 (mean 8.4 features per item) for time 2. The total number of different features generated for the category of living things was 149 (mean 6.5 features per item) for time 1 and 216 (mean 9.4 features per item) for time 2. For the category of nonliving things, the total number of different features generated was 72 (mean 3.6 features per item) for time 1 and 146 (mean 7.3 features per item) for time 2. The number of non-perceptual features increased over time from 62 (mean 1.4 per item) for time 1 to 234 (mean 5.4 per item) for time 2. In contrast, the total number of visual features that DW generated decreased over time from 150 (mean of 3.5 per item) for time 1 to 115 (mean 2.7 per item) for time 2 (see Table 3.6).

Table 3.6. Frequency of different feature types at time 1 and time 2.

	1988			2000		
Feature Type	Living	Nonliving	Total	Living	Nonliving	Total
Visual	102 (68)	48 (67)	150	66 (31)	49 (34)	115
Functional	9 (6)	11 (15)	20	31 (14)	37 (25)	68
Associated Action	11 (7)	4 (6)	15	30 (14)	16 (11)	46
Superordinate	14 (9)	1 (2)	15	24 (11)	5 (3)	29
Others	13 (9)	8 (11)	21	65 (30)	39 (27)	104
Total	149	72	221	216	146	362

Note: Numbers in parenthesis refer to % feature type generated per category

Two feature types (visual and nonperceptual features) captured 90.4% of the total number of properties that DW generated at time 1 and 71.3% at time 2. For time 1 the remaining 9.6% were classified as incorrect/other information (4.1%), tactile (3.6%), similes (1.4%), and taste/smell (0.5%). For time 2 the remaining 28.7% were incorrect/other information (24%), tactile (1.4%), taste/smell (1.4%), similes (1.1%), and sound (0.8%).

The data were analysed using a mixed design ANOVA with Time (1988, 2000) and Feature Type (visual, non-perceptual) the within-stimulus factors, and Category (living, nonliving) the between-stimulus factor. Significant main effects were observed for Category [$F(1, 41) = 17.08$, $p<0.01$], Time [$F(1, 41) = 51.92$, $p<0.01$], and Feature Type [$F(1, 41) = 4.33$, $p<0.05$]. A significant two-way interaction was observed between Time and Feature Type [$F(1, 41) = 89.43$, $p<0.01$]. No other significant interactions were found, although the three-way interaction between Time, Category, and Feature Type approached significance [$F(1, 41) = 3.47$, $p = 0.07$]. Figure 3.6 illustrates that the significant interaction between Time and Feature was found because the number of visual features produced by DW decreased over time, whereas, the number of nonperceptual features increased. The pattern in the three-way interaction occurred because, in addition to the two-way interaction between Time and Feature Type, the number of visual features produced for living things decreased over time (from 102 to 66), whereas the number of visual features produced for nonliving things remained relatively constant (48 and 49 at time 1 and 2, respectively).

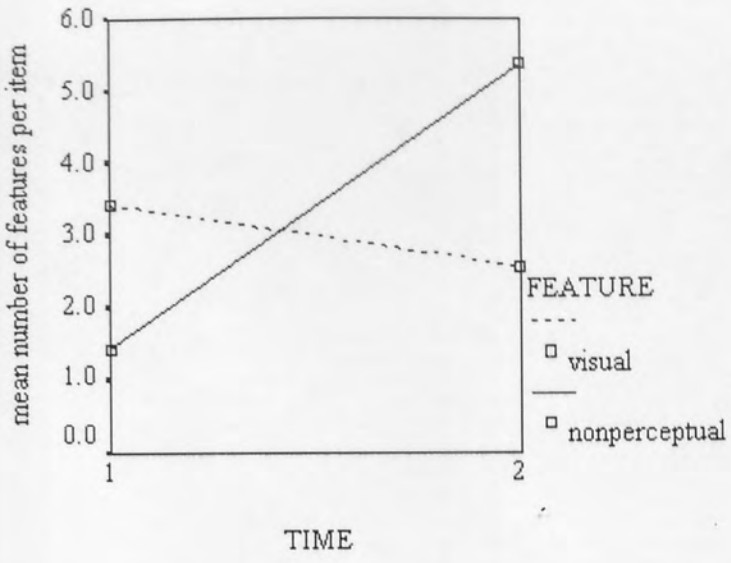
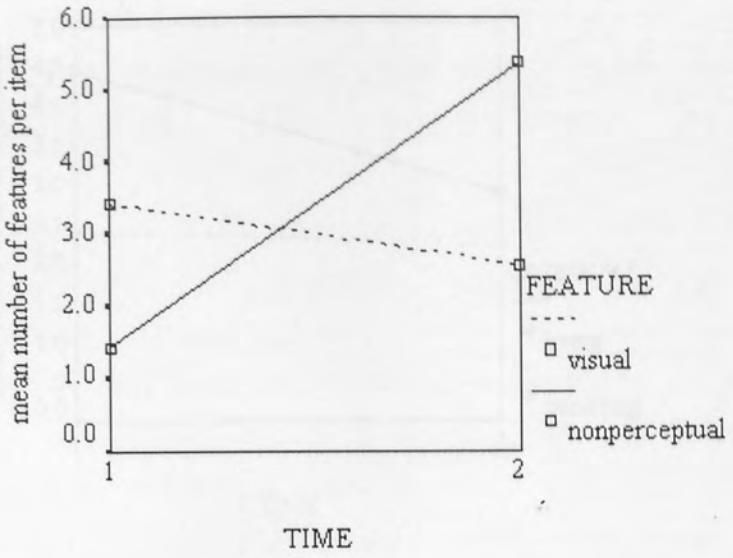


Figure 3.6. The mean number of visual and non-perceptual features generated by DW in the verbal definitions test at both time 1 and time 2.

Discussion

The ability of control subjects to identify DW's definitions more easily at time 2 compared to time 1 contrasts with the deterioration in his performance for drawing from memory (Experiment 8). This indicates that the deterioration in drawing from memory was not a general age-related impairment. The key finding from the verbal definitions experiment is that there was an increase in the number of generated features from all the classified feature types except visual features. The number of visual features decreased from 150 (67.9% total features produced) at time 1 to 115 (31.8% total features produced) at time 2.



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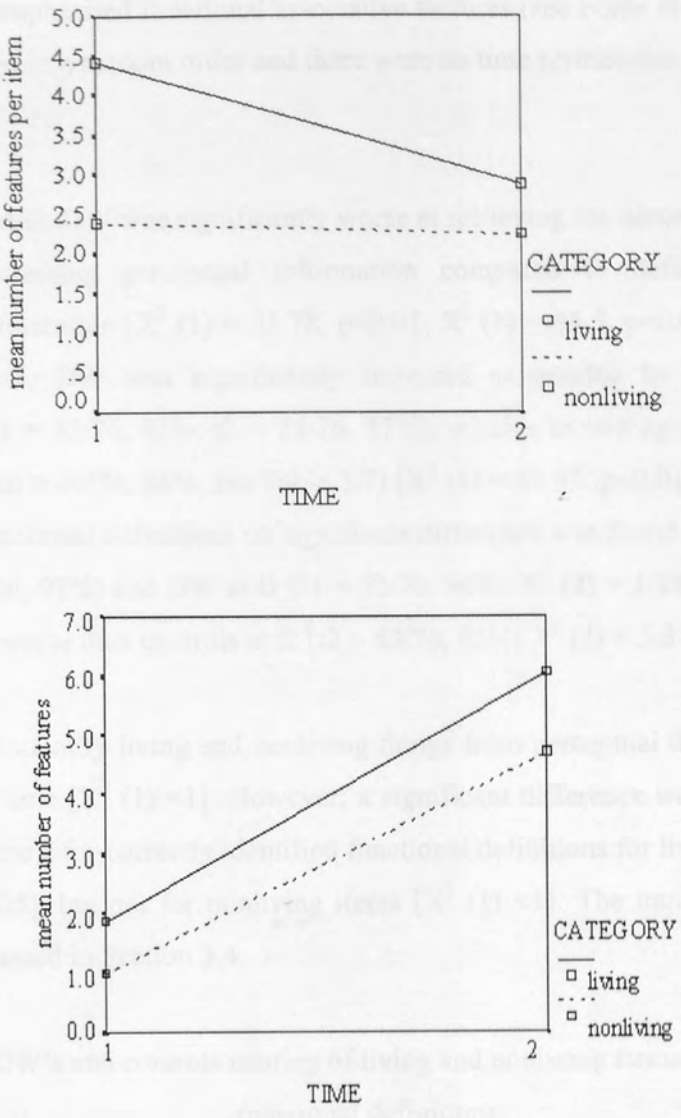


Figure 3.7. The mean number of (a) visual features and (b) non-perceptual features generated by DW for living and nonliving things in the verbal definitions test at both time 1 and time 2.

Experiment 7. Naming from Verbal Definition

Method

In 1988 and 2000 DW was presented with two definitions of the 76 items also presented in the first experiment in this chapter and requested to name the item being defined. Each item had one definition that emphasised visual/perceptual features and

another that emphasised functional/associative features (see Forde et al., 1997). Items were presented in a random order and there were no time restrictions.

Results

At both t1 and t2, DW was significantly worse at retrieving the names of objects from definitions stressing perceptual information compared to definitions stressing functional information [X^2 (1) = 51.78, $p<0.01$; X^2 (1) = 33.5, $p<0.01$, respectively]. At both times, DW was significantly impaired at naming to visual/perceptual definitions (t1 = 32/76, 42%; t2 = 28/76, 37%), relative to two age-matched control subjects (mean = 65/76, 86%, see Table 3.7) [X^2 (3) = 69.67, $p<0.01$]. In contrast, for naming to functional definitions no significant difference was found between controls (mean = 70/76, 92%) and DW at t1 [t1 = 73/76, 96%; X^2 (2) = 1.98, NS] but he was significantly worse than controls at t2 [t2 = 63/76, 83%; X^2 (2) = 5.87, $p = 0.053$].

His ability to identify living and nonliving things from perceptual definitions did not change over time [X^2 (1) <1]. However, a significant difference was found between time 1 and time 2 for correctly identified functional definitions for living items [X^2 (1) = 4.55, $p<0.05$], but not for nonliving items [X^2 (1) <1]. The implications of these data are discussed in Section 3.4.

Table 3.7. DW's and controls naming of living and nonliving items from visual and functional definitions.

	DW Time 1	DW Time 2	Control mean
Living - Visual	11/38	11/38	30/38
Living - Functional	35/38	28/38	35/38
Nonliving - Visual	21/38	17/38	33/38
Nonliving - Functional	38/38	35/38	37/38

Experiment 8. Memory for Size

Method

In 1988 and 2000 DW's ability to make judgements about the real-life size of objects was assessed. He was presented with the spoken names of 40 pairs of stimuli (20 living and 20 nonliving things) and was requested to state which of the pair was larger (e.g. "which is larger? A cow or a goat?"). No time constraints were set.

Results

In 1988 DW scored a total of 38/40 (95%) correct; 18/20 (90%) for pairs of living things and 20/20 (100%) correct for pairs of nonliving things. In 2000, he scored a total of 38/40 (95%) correct; 19/20 (95%) for pairs of living things and 19/20 (95%) for pairs of nonliving things.

Discussion

DW was relatively good at making size judgements form memory. This result contrasts with the findings in experiments 5 and 6 where he performed poorly on tests requiring him to draw upon stored visual knowledge (e.g. drawing from memory). Interestingly, Riddoch et al. (1999) reported a similar result in their follow-up assessment of patient HJA. One reason for this may be that the size judgement task is simply easier than drawing from memory, and reflects a lack of sensitivity inherent in forced-choice tests compared to 'free report' tests such as drawing from memory and verbal definitions. Riddoch et al (1999) suggested that when a subject is forced to choose between two alternative stimuli, even impoverished residual visual knowledge might be adequate for successful performance. Alternatively, memory for size may be stored separately to memory for shape and DW may not have sustained damage to this region. For example, Forde et al. (1997) have shown that a patient (SRB) with a category-specific recognition deficit for living things was able to perform well on tests of size knowledge when stored visual knowledge about the shape of objects was degraded (see also Sartori & Job, 1988).

Experiment 9: Colour Association test

Method

DW was presented with a spoken word and asked to generate the colour of the item for living things (20 items) and nonliving things (21 items), or the colour associated with a word for more abstract concepts (e.g. angry, embarrassed, communist) (10 items). The words were presented in a random order.

Results

DW scored 37/51 (73%) correct at t1 and at t2. His performance remained stable for living things (13/20 at t1 and t2), nonliving things (15/21 at t1 and 14/21 at t2) and abstract words (9/10 at t1 and 10/10 at t2). There was a high degree of consistency of

response between the two assessments [95% for living things, $C = 0.68$, $p<0.01$; 81% for nonliving things, $C = 0.51$, $p<0.01$; 90% for abstract concepts, $C = 0.37$, NS].

Discussion

These results suggest that DW's stored visual knowledge about the colour of objects has remained stable over 12 years. As for size judgements, it is possible that memory for colour is stored separately to memory for shape (Luzzatti & Davidoff, 1994), and therefore, only DW's visual knowledge concerning the shape of living things has deteriorated over the time. Interestingly, DW was able to name most basic colours (he named yellow, blue, red, white, brown, and green correctly) so he does not have a perceptual impairment in processing colour information. This contrasts with his impairment in processing complex overlapping shapes. This suggests that the perceptual deficit in shape processing contributed to the loss of information from long-term memory. Where perceptual encoding was less impaired, there was less evident memory loss over time. Nevertheless, DW was deficient at recalling the colour of objects relative to more abstract concepts. Abstract concepts have verbal links to colour knowledge whilst objects can have visual links (cf Beauvois, 1982). It appears then that these visual links from object concepts to their colours have been disturbed even though basic colour perception (and even colour naming) remained relatively good. The intact perception of colour seems to have been sufficient to maintain those residual visual object-colour associations that remained after his initial lesion.

3.4 GENERAL DISCUSSION

This chapter has reported a longitudinal study on a patient DW with a category-specific agnosia for living things. The extent to which DW's impairment has changed over time was evaluated by comparing data collected in 1988 with his performance on the same tests, using the same stimuli, 12 years later. In particular, his ability to identify pictures and real objects, to draw from memory and to access stored semantic information about living and nonliving things was tested. The main findings were: i) DW was significantly better at identifying real objects compared to line drawings, ii) DW presented with a category-specific impairment for living things, and this remained over a 12-year period, iii) DW's ability to identify real nonliving objects improved over time but his recognition of real living objects remained at floor, iv)

DW's ability to access stored visual knowledge for shape declined over time. These data help to address a number of important questions concerning the cognitive processes involved in object recognition and the links between perceptual and memorial processes. For example, why is visual recognition better for real objects compared to line drawings? Why did DW present with a category-specific recognition impairment for living things? Does perceptual experience help update and/or maintain long-term visual knowledge? These questions are addressed in the following sections.

3.4.1 Recognition of Real Objects

In general, DW presented with a consistent pattern of performance over time for tests that assessed his object recognition abilities. The exception to the stable nature of his performance over the 12-year period was an increased ability to name real nonliving objects from vision (the same pattern as found in other agnosic patients, see Kertesz, 1979; Riddoch et al, 1999; Sparr et al, 1991; Wilson & Davidoff, 1993). The selective improvement in naming real objects but not line drawings suggests that DW did not have a comprehensive recovery of function but was using a compensatory strategy and relying more heavily on visual cues available in real objects but not line drawings. In particular, it was shown that he was not using surface cues such as colour or texture, but was using depth cues (stereo disparity and lateral head movements) to facilitate his naming of real objects.

On the basis of DW's abnormal, part-by-part method of drawing, poor performance on overlapping figures and relatively poor matching of unusual views when the main identifying feature was obscured, it was hypothesised that DW had an 'integrative agnosia' – that is, a perceptual processing impairment that may be related to problems in integrating local object features into perceptual wholes (similar to patient HJA, Riddoch et al., 1999). It is proposed that the depth cues available when viewing real objects facilitated DW's encoding of the relation between surface detail and parts of objects (see also Chainay & Humphreys (2001) for a similar conclusion for patient HJA).

3.4.2 Stored Visual Knowledge

In Experiment 5 deterioration in DW's ability to produce identifiable drawings from memory over time was reported. Two possible explanations were put forward to

explain this performance. First, that a general degradation of ability had occurred over time due to the effects of age and/or general inactivity. However, his ability to access 'low level' visual features (such as size, length and orientation of lines on the BORB tests) indicated that he was able to see the basic components of objects. His ability to copy drawings (albeit in an abnormal fashion) indicated that age had not significantly affected his visuo-motor co-ordination. Furthermore, in additional tests that putatively require access to stored knowledge DW's performance did not decline over time. In Experiment 6 (verbal definitions) he produced a greater amount of information in the present assessment than in the original test, and in experiments 8 (memory for size) and 9 (memory for colour) his performance remained stable over time. The second explanation was that his stored visual knowledge for shape had genuinely deteriorated over time. Consistent with this, there was also a significant decline in the number of visual features DW generated in a verbal definitions test. This deterioration of stored visual knowledge in a patient with a visual/perceptual impairment has implications for the nature of the processes involved in object recognition and memory. The data provide further support for the proposal that without perceptual input 'updating' or maintaining stored visual knowledge, this information will deteriorate over time (Riddoch et al., 1999).

It appears, therefore, that the perceptual and memorial processes involved in object recognition are not functionally independent, and to some degree interact. This finding supports interactive/connectionist accounts of visual object recognition (e.g. Ellis & Humphreys, 1999) rather than accounts that emphasise dissociations between perceptual and memorial processes (e.g. Behrmann et al., 1992). Indeed, in this respect it is interesting to note that DW has reasonable colour perception and his stored knowledge about the colours of objects did not deteriorate over time. Nevertheless, DW did have impaired visual colour knowledge about some objects relative to his verbal colour knowledge associated with abstract concepts. The results show that visual colour knowledge can be disrupted even when there is minimal perceptual impairment in colour processing in a patient (see also Miceli et al. 2001). However, the preserved colour processing appeared sufficient to support colour memory across the 12-year period examined here.

3.4.3 Category-specificity

DW presented with a category-specific impairment for living things that remained over the 12-year period. In Section 3.3 it reported that this was not a result of confounding variables, such as name frequency, visual complexity, and concept familiarity. Therefore, it is proposed that DW's difficulty in recognising living things was, at least in part, a result of his difficulty integrating parts into a coherent whole. Living things tend to have the same parts (head, tail, 4 legs etc) and rather subtle differences in the relative size and scaling of these parts differentiate one object from another. A part-by-part analysis would be sufficient to determine that the object is an animal, but identifying a particular animal may require more holistic, global processing. In contrast, nonliving things tend to have salient and diagnostic parts (e.g. the dial of a telephone) and processing the constituent parts could be sufficient to uniquely identify the object. Consistent with this idea, DW was impaired on a number of tasks that required global processing. For example, in copying line drawings he was able to draw the constituent parts of animals but the size and scaling of parts was inappropriate. He also had difficulty drawing round the overall shape of one object in an overlapping figures test and in identifying an object when the main feature was obscured.

In Section 3.3 it was reported that DW's stored visual knowledge declined over time as observed in the drawing from memory test (Experiment 5), and the verbal definitions test (Experiment 6). This degradation of stored visual knowledge has implications for theories of category-specific impairments. A number of authors have suggested that visual information is more important for distinguishing between living things compared to nonliving things (Humphreys et al., 1988; Warrington & Shallice, 1984). For example, Humphreys et al. (1988) suggested that living things are more structurally similar to one another than nonliving things and identification of living things requires access to more detailed visual information (see Section 1.3.5). This theory predicts that if stored visual knowledge is not updated by visual perception, this will have a greater effect on living compared to nonliving things because the former rely more heavily on visual cues to distinguish a target from competing exemplars (Humphreys et al, 2002). In contrast, for nonliving things, stored functional information, rather than visual knowledge, may be more informative (perhaps critical) for differentiating between one exemplar and another (Warrington & Shallice, 1984;

though see Section 1.3 for examples of alternative views on category-specificity). Consistent with this, DW's ability to draw living things from memory deteriorated more than his ability to draw nonliving things. In addition, when asked to define objects, he recalled fewer visual features of living things at time 2 compared to time 1 but his recall of the visual features of nonliving things remained stable.

Interestingly, when DW was provided with definitions that stressed the visual and functional attributes associated with objects, his performance only declined with functional definitions of living things. How can this be accounted for? Firstly, it is proposed that DW had difficulty in spontaneously accessing stored visual information. However, when given a set of visual features he was able to use his residual knowledge to name some target items from both categories (though overall his performance was relatively poor with visual definitions of both categories and was consistently worse with living things). Secondly, it is proposed that accounts that stress the importance of different types of knowledge for different categories can accommodate the selective decline in his ability to name functional definitions of living things at t2 (73% correct) compared to t1 (92% correct). If living things are represented primarily in terms of visual features and if these important (perhaps even defining) visual features are impaired, then DW may not have enough information to differentiate one exemplar from another – even when given definitions that stress the functional attributes of living things. In other words, when DW is given a functional definition of a living thing, his ability to recognise and name that item depends on his ability to access stored visual information (Humphreys & Forde, 2001).

To illustrate, it was evident from his definition that DW did not know that tigers have stripes. It is suggested that without this knowledge DW does not know what a tiger is, and therefore, is unable to identify this item from a functional definition such as 'a fierce animal of the cat family found in India'. This hypothesis has been supported by recent neuroimaging studies, which show that areas involved in the processing of form are activated when subjects answer questions about the visual and *functional* properties of living things (Chao et al, 1999; Thompson-Schill et al, 1999). It appears that 'knowing' what a living thing is, and being able to answer all kinds of questions about it, depends heavily on being able to access this stored visual information. In contrast, in the imaging studies, activation in form processing area was not enhanced when subjects

answered questions about the functional/categorical properties of nonliving things. Other attributes, such as the function or action associated with an object, may be more important for nonliving things. Consistent with this, Price and Friston (2001) summarise research demonstrating that the left posterior middle temporal region, close to the areas involved in the processing of motion/actions (Martin et al, 1995; Phillips et al, 1999), is the most consistently activated area when subjects are required to recognise nonliving things.

The visual properties of nonliving things may also be relatively preserved as a result of privileged links between visual and functional knowledge for these objects. For example, De Renzi and Lucchelli (1994) suggested that stronger links exist between the visual and functional properties of nonliving things compared to living things (see Section 2.1) because visual properties, such as the overall shape and constituent parts, are directly related to the function of a nonliving object (see Section 2.1 for the related view of Moss et al, 1997; Tyler & Moss, 1997). Nonliving things have been designed and constructed to perform a specific function. Therefore, when stored visual knowledge is degraded over time, intact functional/associative properties of nonliving objects (e.g. is used for hammering) may help up-date and maintain the corresponding visual features (e.g. has a handle, has a heavy end). In contrast, living things have not been designed for a particular function in the same sense as manmade artefacts and, as a result, the nature of the correlations between visual form and function is different. Moss and colleagues have suggested that form-function correlations for living things tend to be between visual features that are common to many living things (e.g. has legs, has ears) and their biological functions (e.g. can run, can hear). Thus, as visual knowledge declines over time, the interactive links between intact functional properties and visual knowledge may only help to maintain information about visual features that are common to many exemplars. Consistent with this, DW was able to describe the generic properties of animals (e.g. has legs, has a tail) but he was unable to recall the specific visual attributes of animals (e.g. that a giraffe has long legs, that a pig has a curly tail).

In summary, it is proposed that the data presented in this chapter provide empirical support for the idea that perceptual and memorial processes interact, and, specifically, that some degree of perceptual input is required to update and maintain stored visual

knowledge concerning the form of objects. The decline in DW's ability to retrieve visual properties of living things compared to nonliving things also provides support for accounts that stress (1) the importance of different types of knowledge for differentiating between exemplars from different categories, and (2) the role of form-function correlations in semantic memory.

CHAPTER 4

THE ROLE OF LOCAL AND GLOBAL PROCESSING IN THE RECOGNITION OF LIVING AND NONLIVING THINGS

4.1 INTRODUCTION

In this chapter local and global processing in object recognition for living and nonliving things was investigated via two case studies on patients (DW and HJA) with integrative visual agnosia. The objectives were to investigate the nature of both patients' visual recognition impairments in more detail and to test if their integrative agnosia could have led directly to their category-specific deficit for living things. This was realised by testing their ability to process local and global information from hierarchical structures. The data has implications for explanations of category-specificity that assume damage is necessary to stored semantic knowledge (e.g. Caramazza & Shelton, 1998; Warrington & McCarthy, 1987; Warrington & Shallice, 1984). The data also has more general implications for understanding the role of local and global processing in visual object recognition, and helped distinguish between three influential theories: 1) the global precedence theory (e.g. see Navon, 1977), 2) the attentional spotlight theory (e.g. see Heinze et al, 1998), and 3) the hypothesis that local processing, global processing and integration of local and global information are mediated by functionally independent systems (e.g. see Lamb et al, 1990). The data from patient DW has been submitted for publication (Thomas & Forde, submitted to Neurocase).

McCarthy and Warrington (1988) stated that 'for a category-specific deficit to emerge in the first place it is necessary that the information should have already been categorised along a semantic dimension' (p. 428). However, it was shown in the previous chapter (see also Thomas et al, 2002) that a category-specific deficit could result from a visual/perceptual processing impairment, rather than problems accessing stored semantic knowledge, and there have been at least three other case studies that showed the same pattern (Arguin et al, 1996 for patient ELM; Funnell, 2000 for patient NA; Riddoch & Humphreys, 1987 for patient HJA). In particular, these category-specific impairments (all for living things) were attributed to deficits in low-level visual/perceptual processing (Funnell, 2000), integrating the structural features of objects (Arguin et al, 1996; Arguin et al, 2002), and integrating local features into a

coherent whole (i.e., integrative visual agnosia) (Riddoch & Humphreys, 1987; Thomas et al, 2002).

In the previous chapter it was suggested that DW's integrative agnosia led to his category-specific impairment for living things because recognition of these items may be more dependent on processing the overall shape of the object rather than the constituent parts. For example, animals tend to have the same constituent parts (e.g. head, 4 legs, body, tail) and it is the relative size and scaling of these parts that distinguishes one animal from another. Fruit and vegetables typically have only one 'part' and recognition of these items depends on accessing the overall shape (e.g. distinguishing between an apple and a pear is based on one object having a tapered end while the other is round). In contrast, nonliving things (e.g. tools, kitchen objects) have more distinctive parts that have been designed for a specific use, and the overall shape of the item is less important (for this argument, see also Sacchet & Humphreys, 1992; Forde, 1999). Consistent with this, the feature-norm experiment in Chapter 2 showed that a significantly greater number of distinctive features were generated for nonliving compared to living things (see also Garrard et al, 2001; McRae & Cree, 2002).

Therefore, the initial motivation for the work reported in this chapter was to test both patients' local and global processing more systematically in selective (Experiment 1) and divided (Experiment 2) attention tasks using hierarchical letters (see Figure 4.1). However, as mentioned previously, the data also have important implications for theoretical models of local and global processing, and, in the following section, three influential theories from this literature were reviewed as background to Experiments 1 and 2.

4.2 Local and global processing

Object recognition is a complex task that requires parsing and representation of information about objects at various levels. For instance, it appears that features need to be analysed at both a local and global level if the object is to be successfully recognised. Local features may be viewed as the small-scale parts or detailed aspects of an object, in contrast to the whole or global aspect that gives the overall form its shape. In one of the seminal studies on local and global processing, Navon (1977)

presented subjects with hierarchical letters that consisted of large (global) letters formed from small (local) letters (see Figure 4.1). On some trials, subjects were asked to detect target letters at the local level and on other trials they were asked to detect targets at the global level. Navon found that subjects were faster at identifying the global letters compared to the local letters. In addition, he reported a global-to-local interference effect i.e., when required to identify the local letter, subjects' response times were slower if the global letter was incongruent with the local letter (e.g. H/s). In contrast, when subjects were required to name the global letter, response times were equivalent when the local letters were congruent (e.g. H/H) and incongruent. These findings led Navon (1977) to propose that global processing occurred before local processing in object recognition, a theory he named 'global-precedence'.

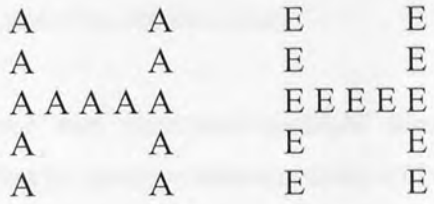


Figure 4.1. This figure illustrates examples of the Navon-type stimuli used in the present chapter.

Since the publication of this work, numerous studies have used similar hierarchical letters to study local and global processing (see Kimchi, 1992 for a review). In many of these studies, subjects showed a global precedence effect (e.g. Boer & Keuss, 1982; Grice et al, 1983; Navon & Norman, 1983; Pomerantz, 1983) but there are also a number of studies where this effect was eliminated or even reversed when the size of the visual angle was changed (Lamb & Robertson, 1990), low spatial frequencies removed (Michimata et al., 1999), number of local elements increased (Martin, 1979), information degraded (Hoffman, 1980), perceptual grouping manipulated (Han et al, 1999), or the attentional salience of local elements increased (Han & Humphreys, 1999).

Furthermore, Heinze et al (1998) found a contrasting pattern of results to Navon (1977) even when similar stimuli were used. For instance, stimuli subtended a similar

visual angle (2.5 and 3.2, in Heinze et al. (1998) and Navon (1977), respectively), and neither study varied in terms of any of the aforementioned differences shown to affect response speed. Heinze et al found that there was no difference in the reaction times when subjects were asked to selectively attend to either the local or global level, but they did find local-to-global interference to be significantly greater than global-to-local interference. Heinze et al argued that when attention is directed to the global level the attentional 'spotlight' is widened and encompasses both local and global elements. In contrast, when attention is directed to the local level, the attentional spotlight is narrowed, gating global form information. Therefore, local information can interfere with processing of the global structure, but global information does not interfere with local level processing. In contrast to Navon's global precedence theory, the attentional spotlight theory predicts that subjects should always show local-to-global interference in selective-attention tasks.

Both 'global precedence' and 'attentional spotlight' theories imply that the direction of the interference effect in selective attention tasks will co-vary with the level that is processed preferentially. However, in a series of neuropsychological studies, Lamb and colleagues challenged this assumption and suggested that there may be functionally independent components for local processing, global processing and integration of information from both levels (Lamb et al, 1989; Lamb et al 1990; Robertson et al, 1988). Lamb et al (1989) found dissociations between local and global processing in patients with left and right hemispheric damage. Patients with temporal cortex lesions in the left hemisphere were faster at detecting letters at the global level compared to the local level, but this global response time advantage significantly decreased for patients with temporal lesions in the right hemisphere. Interestingly, in contrast to normal subjects, Lamb et al (1989) also reported that both right and left hemisphere damaged patients showed no interference effects i.e., even though patients with left-hemisphere lesions identified global letters faster than local letters they showed no global-to-local interference. Lamb et al outlined two possible explanations for the patients' lack of interference in the selective-attention task: 1) The ability to process information simultaneously from both levels was impaired, resulting in an increased ability to selectively attend to a single stimulus level without unwanted interference. 2) Patients, like normal subjects, were able to simultaneously

process information from the attended level and the to-be-ignored level, but were unable to integrate information into a coherent perceptual whole.

To test these alternative accounts, Lamb et al (1990) conducted a divided-attention test on the same patient groups. Patients were asked to judge if a target letter appeared at either the local or the global level on a particular trial and were, consequently, forced to process information at both levels. The authors argued that if interference occurred under these conditions, it would indicate that patients were not processing information simultaneously in the selective attention task. If, however, there were still no interference effects it would indicate that patients were unable to integrate information from the two levels. No interference effects were found. Accordingly, Lamb et al (1990) suggested that, unlike normal subjects, the patient groups were unable to integrate local and global level information. They proposed that, because the direction of the interference effect did not co-vary with the efficiency with which patients could process local and global information, there must be separate mechanisms for processing local information, global information and for integrating local and global information. In particular, they suggested that the left and right posterior temporal lobes are primarily responsible for processing local and global information, respectively, and information from both levels is integrated in the posterior superior temporal lobe. In addition, they suggested that a fourth mechanism, in the rostral inferior parietal lobe, directed attention between local and global processing.

There are, therefore, three contrasting theories of local and global processing tested in this chapter:

1. The global precedence theory predicts that subjects should be faster at processing global information and should show a global-to-local interference effect (Navon, 1977).
2. The attentional spotlight theory predicts that subjects should show local-to-global interference effects but not global-to-local interference effects (Heinze et al., 1998).
3. Lamb and Robertson's (1990) theory proposed that different mechanisms mediate local processing, global processing and the integration of information at these two

levels. It should, therefore, be possible to find dissociations between these three processes.

4.3 CASE REPORT

Patient DW

A general neuropsychological assessment of patient DW was described, along with his visual/perceptual abilities and impairments, in the previous chapter (see section 3.2). Hence, only the background data most relevant to the following experimental investigations is summarised here. DW scored within the normal control ranges on tests of low-level visual processing (see Table 3.1). However, he had impairments at separating figure from ground in overlapping pictures (BORB, test 6, see Table 3.2). In a further test of figure-ground segmentation, one drawing was superimposed onto another and he was asked to draw around the outline of one of the two pictures. The two pictures were from the same superordinate category. Successful completion of this task requires the ability to group the different parts of one object together while concurrently ignoring the parts of the other. DW had considerable difficulty with this task and was only able to correctly outline 14/37 (38%) of the items. DW also had difficulties copying line drawings and adopted an abnormal 'piecemeal' strategy, characteristic of integrative agnosia (see Riddoch & Humphreys, 1987). For example, in copying a picture of a horse (see Figure 3.1) he drew the front legs first, followed by the back legs, then the head and, consequently, although each part was competently copied, difficulties emerged when he attempted to join up the parts as a whole.

DW's performance on tests of object constancy (i.e., the ability to judge that an object remains the same when viewed from different positions) was normal when objects were rotated in depth (foreshortened view test, BORB test 8) but just outside the control range when one picture was rotated so that the main identifying feature was obscured (minimal-feature view test, BORB test 7) (see Table 3.1). In 1988, DW also performed at a normal level on a foreshortened views test (30/32, 94%) with photographs, and slightly worse on minimal features views (28/32, 88%). This pattern of poorer performance on the minimal features task compared to the foreshortened view task is unusual (Riddoch & Humphreys, 1993) and suggests that DW may have used local features to identify objects. Minimal features views were difficult for him

because important local features are obscured but objects in foreshortened views were still identified because the main features remained visible.

DW showed a marked category-specific impairment and was significantly worse at naming line drawings of living items (2/38, 5.3%) compared to nonliving items (21/38, 55.3%) [X^2 (1) = 20.53, $p<0.01$] (BORB test 14). The majority of his errors were visually, or visually and semantically, related to the target (38% of his errors). For example, DW called a mushroom an "umbrella", and for celery said "it is a whisk, the end looks like a whisk". On a number of occasions it was clear that DW could see individual features and was trying to use these to guide his naming. For squirrel he said "I though a cat but the tail has put me off", for giraffe he said "horse, but the legs are not long enough .. maybe a cow, but no udder .. an animal", for owl he said "an animal .. a bird .. I know it is a bird because of the feet". His other responses tended to be "don't know" (28%), or superordinates (23%), although he also made a few categorically related errors (11%),

In summary, it appeared that DW had no impairments to basic visual/perceptual processing (e.g. in processing length or orientation of lines) but showed a number of the defining features of integrative agnosia: (1) a piecemeal procedure in copying; (2) poor performance on tests with overlapping figures (3) difficulty recognising an object when the main feature is obscured. DW's difficulty in naming line drawings of real objects seemed related to his visual/perceptual processing problems, rather than a semantic or name retrieval impairment, and the majority of his errors were visually related to the target.

Patient HJA

HJA was 80 years old at the beginning of the present investigations (01-04-01). A right-handed man, he suffered a posterior cerebral stroke perioperatively in 1981 resulting in a dense visual agnosia, prosopagnosia, alexia without agraphia, achromatopsia and topographical impairments (Riddoch et al, 1999). A CT scan (May 1981) failed to reveal any marked neurological abnormalities, but a subsequent MRI scan in 1989 showed bilateral lesions of the inferior temporal gyrus, lateral occipitotemporal gyrus, the fusiform gyrus, and the lingual gyrus. Patient HJA was brought in for experimental testing as a result of the observed similarities between the

two patients (i.e., both were described as integrative agnosics, with category-specific impairments for living things). As a consequence, only HJA's performance on the local and global processing experiments was assessed in the present chapter, however, over the past twenty years, his impairments have been described in a number of studies by Humphreys and colleagues (Humphreys & Riddoch, 1984; Humphreys et al, 1988; Riddoch & Humphreys, 1987; Riddoch et al, 1999).

4.4 EXPERIMENTAL INVESTIGATIONS

4.4.1 Experiment 1. Selective-Attention

4.4.1.1 Method

DW, HJA and eight age-matched control subjects were tested. Control subjects (5 female, 3 male) ranged in age from 56 to 69 years [mean = 65 years], and had normal, or corrected to normal vision. Subjects were presented with compound letter stimuli constructed of large (global) capital letters that in turn were constructed of small (local) capital letters. Global letters were constructed from local letters in a 5 x 5 matrix (see Figure 4.1). There were 16 stimuli constructed from all combinations of letters A, E, S, and H (H/H, H/S, H/E, H/A, A/A, A/S, A/E, A/H, S/S, S/E, S/A, S/H, E/E, E/S, E/A, E/H). On each trial a compound letter stimulus was centrally presented on a Toshiba laptop computer. Letters were presented in black, on a light grey background. Both global and local letters were approximately 1.5 times as tall as they were wide. Global letters subtended 2.5° vertically at a viewing distance of 50cm.

Each task consisted of a set of 16 runs of the 16 stimuli. The subject was required to indicate whether a target letter (H, A, E, or S) had appeared at a target level (local, global) by pressing a designated key on the keyboard for 'yes' (using the right index finger) and 'no' (using the left index finger). Only one letter was target per run. Each stimulus was presented on-screen until a response was received. A 2000ms inter-trial interval then occurred. Stimuli were presented in a pseudorandom order with at least one non-target stimulus occurring after a target stimulus. A Latin-square design was used to order the target stimuli and the target level. Prior to a run each subject was instructed to which target level and letter they were required to respond 'yes' to. Both accuracy and speed of response were emphasised.

4.4.1.2 Results

DW, HJA and control subjects made few errors (3%, 7% and 1.8%, respectively), therefore, response time data was analysed to assess local and global processing. Outliers more than 2.5 SD's away from the mean were removed from the analysis (1.5%, 0.8% and 1.1% for DW, HJA and controls, respectively).

The results from DW, HJA and controls (see Figure 4.2) were analysed separately using three 2-way between-items ANOVAs on response times to items with target level (local vs. global) and congruency (congruent vs. incongruent) the between-item factors. For DW, there was a main effect for level [$F(1, 60) = 24.03$, $p<0.01$]. He was faster at identifying local [818.9ms] compared to global letters [1116.4ms]. No interaction between level and congruence was found signifying that there was no significant interference effect for DW in either direction. HJA showed the same pattern of results: A main effect for level [$F(1, 60) = 5.85$, $p<0.05$]. He was faster at identifying local [628.7ms] compared to global letters [761.9ms]. No interaction between level and congruence, signifying that there was no significant interference effect for HJA in either direction.

For control subjects, there was a main effect for level [$F(1, 60) = 4.60$, $p<0.05$]. They were faster at identifying local [607.1ms] compared to global letters [642.1ms]. There was also a main effect for congruence [$F(1, 60) = 4.82$, $p<0.05$]. They were faster at identifying congruent [606.7ms] compared to incongruent letter pairs [642.5ms]. In addition, a significant interaction between level and congruence was found [$F(1, 60) = 5.61$, $p<0.05$]. Controls showed a significant local-to-global interference effect (mean 74.4ms faster in congruent condition) but a negligible global-to-local interference effect (2.8ms slower in the congruent condition).

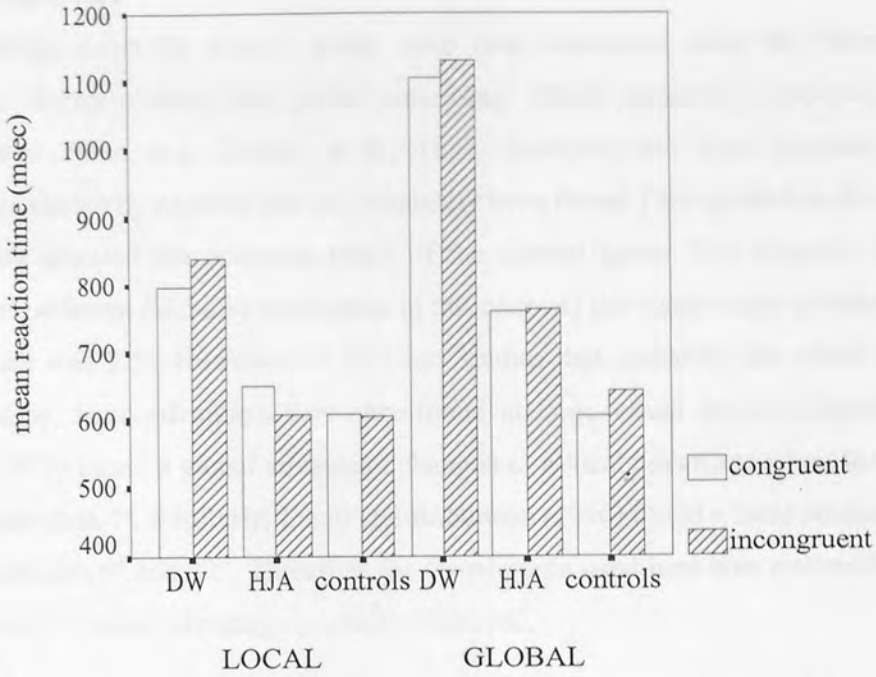


Figure 4.2. This figure illustrates the mean reaction times (msec) for DW, HJA, and controls to target letters at local and global levels both when the target letter is congruent and incongruent with the non-target level letter.

The data indicated that DW, HJA, and controls were slower at accessing global shapes. The relative difficulty for global processing was, however, more pronounced for DW and HJA. The difference between local and global letters was 8.5 times greater for DW compared to controls, and 3.8 times greater for HJA compared to controls. In a 3-way between-items ANOVA with the factors subject (DW, HJA, controls), target level and congruency, there was a significant interaction between level and subject [$F(1, 180) = 7.56$, $p<0.01$] confirming that the difference between both DW's and HJA's response times for local and global stimuli (297.5ms and 133.2ms respectively) were significantly greater than the difference for the control group (35ms). In fact, post hoc comparisons showed that significant differences were found between all levels: DW and controls ($p<0.01$), HJA and controls ($p<0.05$) and DW and HJA ($p<0.01$).

4.4.1.3 Discussion

The findings from the control group were most consistent with the 'attentional spotlight' theory of local and global processing, which predicted a local-to-global interference effect (e.g. Heinze et al., 1998), however, the local response time advantage shown by controls has not frequently been found. Perhaps factors described previously affected the response times of the control group. For example, in the present experiment (and all experiments in this chapter) the visual angle subtended by the stimuli was 2.5°. However, in previous studies that examined the affect of the visual angle, local advantage was only found at large visual angles; Kinchla and Wolfe (1979) found a global advantage changed to a local advantage when the angle was greater than 7°. Similarly, Lamb and Robertson (1990) found a local advantage at angles between 6° and 12°. Therefore the visual angle used here was well within the range where a global advantage is usually observed.

Another possible contributing factor is the age of the control group. For example, a number of studies investigating the effect of age on hierarchical stimuli processing have found a local advantage in older subjects (Slavin et al, 2002; Polster & Rapcsak, 1994; Massman et al, 1993). However, other studies on older subjects found global precedence (Akshoomoff et al, 1993; Bruyer & Scailquin, 2000; Sullivan, 1999; Roux & Ceccaldi, 2001). The visual angle used in some of these studies can explain the findings. For example, Massman et al used a large visual angle of 6.5°. However differences in visual angle cannot account for all the data. Slavin et al (2002) carried out the same experiment on a group of young adults and found global precedence. Slavin et al suggested that the finding of local precedence for their age-matched control group could be attributed to the relative sizes of the stimuli used (global stimuli were 59mm in height and varied between 14 and 31mm in width, local stimuli were 4mm in height and 3mm in width), or the sparseness of the local elements (global stimuli consisted of a minimum of 16 and a maximum of 20 local elements), to which, they argued, older subjects may be particularly sensitive.

DW's impairment for global processing was significantly greater than HJA's which, in turn, was significantly greater than the control group's. DW and HJA were significantly faster at identifying the local target but, in contrast to control subjects, they showed no local-to-global interference effect. This pattern of performance (local

advantage but no local-to-global interference) has also been reported in patients with lesions to the superior temporal gyrus in the right hemisphere (Lamb et al, 1989; 1990). Lamb and colleagues outlined two possibilities to explain the lack of interference in these patients: 1) Patients were abnormally good at selectively attending to the target level and, consequently, were able to ignore information from the other level. 2) Patients attended to both levels simultaneously but were unable to successfully integrate local and global information. In Experiment 2, DW and HJA were tested in their ability to simultaneously process information from both levels and to integrate local and global information in two divided attention tasks. In one condition, they were asked to attend simultaneously to both local and global information and to judge if a target appeared at *either* level. In a second condition, they were specifically required to integrate information from both levels and determine if a target letter appeared at *both* the local and global level.

4.4.2 Experiment 2. Divided-Attention

4.4.2.1 Method

The stimuli and paradigm were the same as Experiment 1 except that subjects were required to indicate whether a target letter had appeared at 'either' level in the first condition, and 'both' levels in the second condition.

4.4.2.2 Results

DW, HJA, and control subjects made few errors (3.9%, 4.7%, and 1.7%, respectively). Reaction time data was, therefore, analysed to assess subject's local and global processing. Outliers more than 2.5 SD's from the mean were removed from the analysis (1.8%, 7%, and 0.9% for DW, HJA, and controls, respectively).

Reaction time data for 'either' condition

The data were analysed using three separate between-items ANOVAs for DW, HJA, and controls on response times to items with target position (congruent, local only, global only) the between-item factor. The ANOVA produced a main effect of target position for DW [$F(1, 45) = 16.57$, $p<0.01$], HJA [$F(1, 45) = 4.43$, $p<0.05$], and controls [$F(1, 45) = 21.97$, $p<0.01$]. For DW, mean response times were ordered: [congruent (860.9ms) < local (1035.6ms) < global (1241.3ms)]. For HJA, mean response times were ordered: [congruent (790.2ms) < local (972.6ms) < global

(1046.7ms)]. For both patients, post hoc multiple comparisons showed significant differences between congruent stimuli pairs and local target stimuli, and congruent stimuli pairs and global target stimuli. For DW a difference was also found between local and global target stimuli, but this was not the case for HJA (Tukey HSD, all $p<0.01$). For control subjects, mean response times were ordered [congruent (622.7ms) < global (750ms) < local (766.8ms)]. Post hoc multiple comparisons showed significant differences between congruent stimuli pairs and local target stimuli, and congruent stimuli pairs and global target stimuli, but not between local and global target stimuli (Tukey HSD, all $p<0.01$).

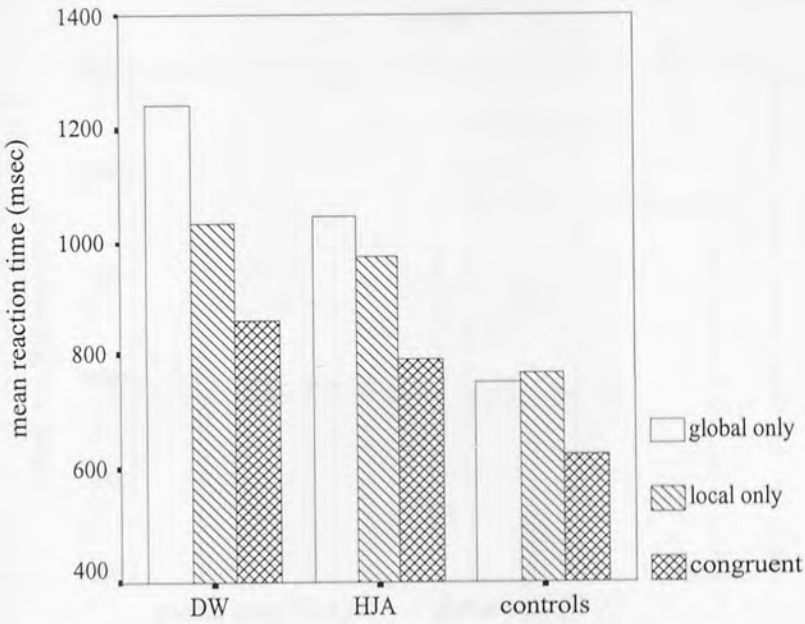
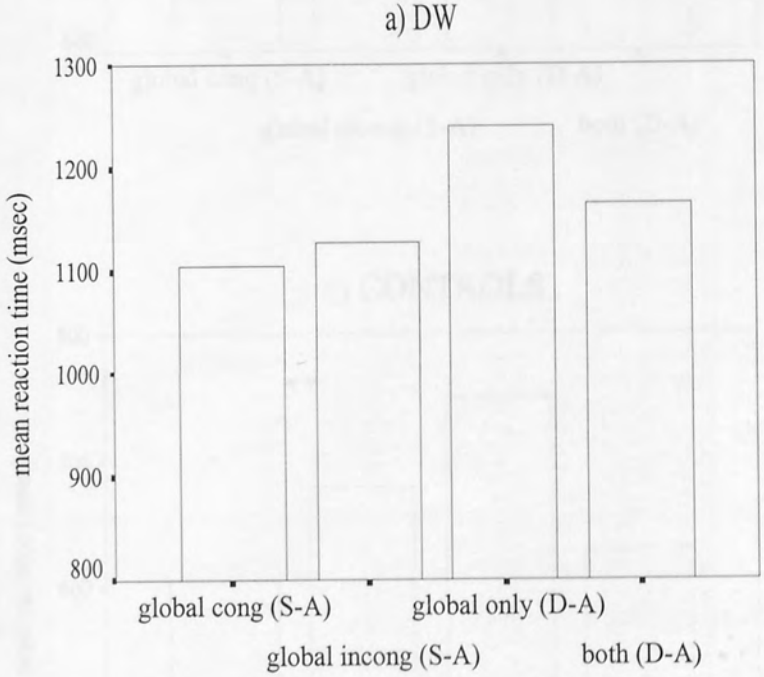


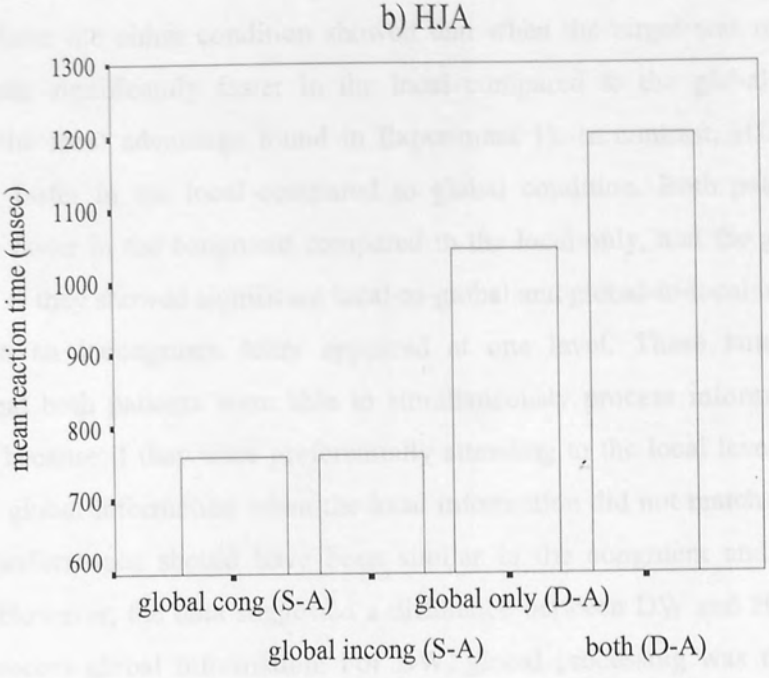
Figure 4.3. This figure illustrates the mean reaction times (msec) for DW, HJA, and controls to target letters at global-only, local-only, and both levels in the 'either' condition in Experiment 2 (divided-attention).

Reaction time data for 'both' condition

The data were analysed using three separate between-items ANOVAs for DW, HJA, and controls on response times to items with the following four conditions; 1) selective-attention (global target congruent), 2) selective-attention (global target incongruent), 3) divided-attention, either level (global-only), and 4) divided-attention both levels (target at both levels). The ANOVA produced a main effect of condition for HJA [$F(1, 60) = 22.73$, $p<0.01$], but not for DW [$F(1, 60) = 1.16$, NS], or

controls [F (1, 60) = 2.61, NS]. For HJA, mean response times were ordered: [global congruent (760.4ms) < global incongruent (763.4ms) < either (global-only) (1046.7) < both (1203.3ms)]. Post hoc multiple comparisons showed significant differences between both and all other conditions, and between either (global-only) and all other conditions (Tukey HSD, all $p<0.01$). For DW, mean response times were ordered: [global congruent (1104ms) < global incongruent (1128.7ms) < both (1166ms) < either (global-only) (1241.3ms)]. For controls, mean response times were ordered: [global congruent (604.9ms) < both (629.4ms) < global incongruent (679.3ms) < either (global-only) (750ms)].





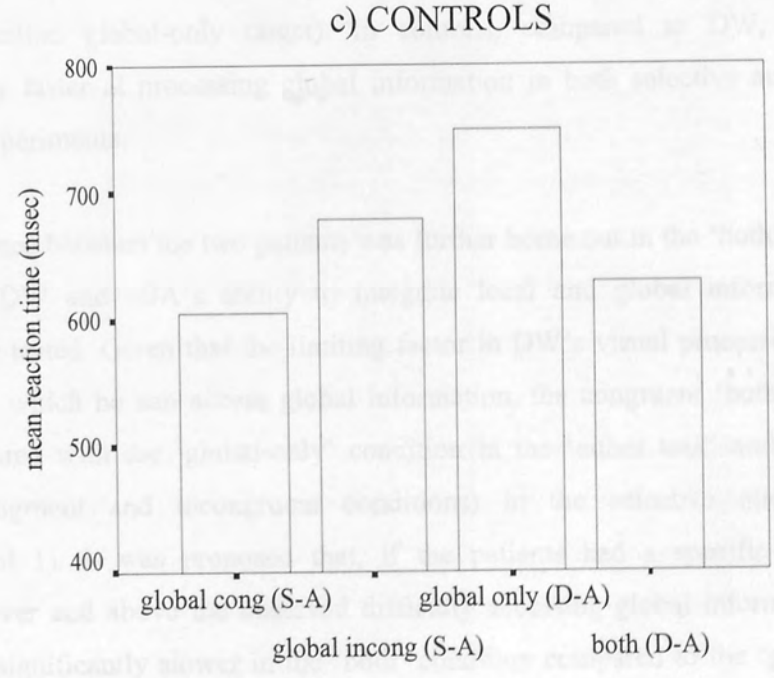


Figure 4.4. This figure illustrates the mean reaction times (msec) for a) DW, b) HJA, and c) controls to target letters in four conditions: 1) selective-attention (global target congruent), 2) selective-attention (global target incongruent), 3) divided-attention, either level (global-only), and 4) divided-attention both levels (target at both levels).

4.4.2.3 Discussion

The results from the either condition showed that when the target was only at one level DW was significantly faster in the local compared to the global condition (replicating the local advantage found in Experiment 1). In contrast, HJA was not significantly faster in the local compared to global condition. Both patients were significantly faster in the congruent compared to the local-only, and the global-only conditions, i.e. they showed significant local-to-global and global-to-local interference effects when an incongruent letter appeared at one level. These latter findings suggested that both patients were able to simultaneously process information from both levels, because if they were preferentially attending to the local level (and only attending to global information when the local information did not match the target), then their performance should have been similar in the congruent and local-only conditions. However, the data suggested a difference between DW and HJA in their ability to process global information. For DW, global processing was the limiting factor to his performance; when the task required global processing, performance was similar regardless of the nature of the task (e.g. selective-attention global target, or divided-attention global-only target). In contrast, compared to DW, HJA was significantly faster at processing global information in both selective and divided-attention experiments.

The difference between the two patients was further borne out in the 'both' condition, in which, DW and HJA's ability to integrate local and global information was specifically tested. Given that the limiting factor in DW's visual processing was the speed with which he can access global information, the congruent 'both' condition was compared with the 'global-only' condition in the 'either task' and the global target (congruent and incongruent conditions) in the selective attention task (Experiment 1). It was proposed that, if the patients had a specific integration problem, over and above the observed difficulty accessing global information, they should be significantly slower in the 'both' condition compared to the 'global only' conditions. This was the case for HJA, but not for DW, suggesting that DW was able to integrate local and global information when required. However, HJA was significantly slower in the 'both' condition compared to the 'global only' conditions, and therefore showed a clear impairment integrating local and global information, over and above any possible global processing difficulty.

Control subjects showed a different pattern of results in the divided attention experiment. In the 'either' condition, they showed no significant difference in their ability to detect a target letter at the local or global level and, as expected, they were significantly faster in the congruent condition compared to local-only and global-only conditions. Control subjects were, however, slightly faster at detecting targets in the global-only compared to the local-only. This showed that DW had a genuine impairment processing information at the global level and was not simply always slower in the most difficult condition.

In summary, the data suggested that DW had a specific difficulty processing the global shape of objects, and that HJA had difficulty integrating information from the local and global levels. In contrast to the selective attention task (Experiment 1), the data from the divided attention tasks showed that DW could integrate when forced to in an experimental situation. It appears that the lack of interference observed for DW in the selective-attention task might be due to an impairment in an attentional system that is abnormally biased to the local level. This idea is discussed in more detail in the General Discussion of this chapter (Section 4.5).

4.4.3 Experiment 3: Naming silhouettes

As reported in Section 4.2, DW and HJA both had a category-specific impairment for living things in a task that required them to name line drawings. A number of studies have shown that control subjects also tend to find living things more difficult to identify than nonliving things. For example, Humphreys et al (1988) found that control subjects named nonliving things (852.5msec) significantly faster than living things (942.5msec), and this pattern has subsequently been simulated in a computer model of object recognition (Humphreys et al, 1995). Humphreys et al (1988) suggested that living things are inherently more difficult to visually recognise and name because they belong to structurally similar categories (see Section 1.3.5). As a result, a picture of a living thing (or the object itself) will activate a number of structurally similar neighbours and create competition for selection within the object recognition and naming system. In contrast, nonliving things tend to be structurally distinct from one another, and consequently, activate fewer competitors in object recognition tasks (Humphreys et al, 2002). Experiment 3 was designed to assess whether the normal advantage for nonliving things would be reversed when local

features were obscured in silhouettes. If the hypothesis that the relative importance of global and local processing differs for living and nonliving things is correct, control subjects should find it more difficult to name silhouettes of nonliving things compared to living things.

4.4.3.1 Method

DW, HJA and 10 control subjects were presented with 74 silhouettes (36 living and 38 nonliving, 2 body parts were removed from the 'living set'), created by filling-in the line drawings in BORB Test 14. The silhouettes were presented one at a time and subjects were asked to name them. No time constraints were set.

4.4.3.2 Results and discussion

HJA's category-specific deficit for living things disappeared when the same items were used but local features obscured, in silhouettes [L = 9/36 (25%), NL = 11/38 (29%) X^2 (1)= 0.44, NS]. This was due to a differential reduction in the number of correctly identified nonliving compared to living things. When presented with silhouettes of nonliving things, HJA's identification was poorer (11/38, 29%) compared to the same line drawings (24/38, 63%) (X^2 (1) = 9.0, $p<0.01$). Similarly, DW's deficit for living things was reduced when he identified silhouettes, although it did not disappear altogether [L = 5/36 (13.9%), NL = 13/38 (34.2%) X^2 (1)= 4.15, $p<0.05$]. Again this was due to a differential reduction in the number of correctly identified nonliving compared to living things. When presented with silhouettes of nonliving things, DW's identification was poorer (13/38, 34%) compared to the same line drawings (21/38, 55%), although this failed to reach statistical significance (X^2 (1) = 3.5, $p=0.07$).

Importantly, control subjects were also worse at naming silhouettes of nonliving (25.9/38, 68%) compared to living things (27.6/36, 77%), [F (1,9) = 18.9, $p<0.01$]. These data provide more direct evidence for the hypothesis that the relative importance of global versus local information differs for living and nonliving things. In particular, they are consistent with the idea that overall shape is more important in the recognition of living things, but local features are more important for nonliving things. When local features were obscured in silhouettes, there was more of a

detrimental effect for nonliving things for both DW and HJA, and the normal advantage control subjects showed when naming these items was reversed.

4.5 GENERAL DISCUSSION

In this chapter two case studies of patients with integrative visual agnosic and a category-specific impairment for living things were reported (see also Chapter 3 and Thomas et al, 2002 for details of DW; Riddoch et al, 1999 for details of HJA). The initial aims of the experimental investigations were to assess DW and HJA's local and global processing in more detail (in Experiments 1 and 2) and to test whether the importance of local and global processing differed for living and nonliving things (Experiment 3). However, the data from Experiments 1 and 2 also had implications for theoretical models of local and global processing. As a consequence, the following section discusses how the data could be used to test three influential theories of local and global processing before some conclusions are drawn about the possible links between local and global processing and the recognition of living and nonliving things.

Local and global processing

The data from Experiments 1 and 2 were used to test the predictions from three contrasting theories of local and global processing. (1) The global precedence theory suggested that global information is processed before local information in object recognition (Navon, 1977). According to this account, local and global information is processed by a single mechanism and global information automatically interferes with local processing. This theory predicted that in selective attention tasks, subjects should be always be faster at detecting global information and should show a global-to-local interference effect. (2) Heinze et al (1998) outlined an 'attentional spotlight' theory of local and global processing that predicted the opposite pattern in selective attention tasks. According to this account, when subjects are attending to global information the spotlight is widened and automatically processing local information, which can interfere with global processing. When subjects are attending to local features, however, the spotlight is relatively narrow and may not incorporate global information. Heinze et al (1998) predicted that subjects should show local-to-global, but not global-to-local, interference effects in selective attention tasks. (3) Lamb and Robertson (1990) suggested that functionally (and anatomically) different

mechanisms mediate local processing, global processing and the integration of information at these two levels. This theory predicted that patients could show preferential processing of global information (but no global-to-local interference effect, as suggested by Navon, 1977) or local information (but no local-to-global interference effect, as suggested by Heinze et al, 1998).

In a selective attention task (Experiment 1), it was found that control subjects were significantly faster at processing local information and showed a reliable local-to-global interference effect. The data are consistent with Heinze et al's (1998) attentional spotlight theory and challenged the idea that global information is necessarily processed before local features (Navon, 1977). DW and HJA were also significantly faster at processing local information. Indeed, it was proposed that DW was abnormally poor at accessing global information, as the difference between his reaction times for local and global targets was 8.5 times greater than for controls. However, despite both patients' marked advantage for local information, they did not show a local-to-global interference effect. This is difficult to explain in terms of an attentional spotlight theory and, overall, the data are most consistent with Lamb and Robertson's suggestion that local processing, global processing and the integration of this information are mediated by separate mechanisms.

In a divided attention task, DW and HJA were required to attend to local and global information simultaneously, and under these conditions an interference effect was found. They were faster when the target letter appeared at both local and global levels compared to local-only or global-only conditions. To account for the different pattern of results in the selective and divided attention tasks, it was suggested that DW showed an abnormal bias to local features, and that HJA had an impairment integrating local and global information. In the selective attention tasks DW was biased to local stimuli, but when cued to attend to both levels, and forced to divide his attention, he was able to simultaneously process and integrate local and global information. In the selective attention tests, HJA also showed a bias to local information (although less pronounced that DW), and in the 'either' divided attention task HJA was able to simultaneously process local and global information. However, he was significantly slowed in the 'both' divided attention task, which indicates an impairment when the task required him to integrate information.

One further point to note is that, although the 'paper and pencil' tests used to assess the abilities of patients DW and HJA (e.g. drawing from memory, copying) resulted in them both being classified as 'integrative agnosic', a more detailed analysis of their local and global processing revealed differences in their performance. As discussed earlier, DW had an attentional bias towards local information that resulted in difficulty processing global information, whereas HJA had a perceptual problem integrating local and global information. Therefore, the data indicate that standard paper and pencil tests are not sufficient to differentiate between patients with 'integrative visual agnosia'. Interestingly, however, both DW and HJA's visual/perceptual problems led to difficulties recognising living compared to nonliving things, and the reason for this is discussed in the next section.

The role of local and global processing in the recognition of living and nonliving things

As discussed in Section 4.1, category-specific impairments for living and nonliving things are almost always interpreted in terms of damage to stored semantic knowledge. Indeed, some authors have assumed that because the impairments are category-specific in nature this implies that the impairment *must* be at a semantic level (McCarthy & Warrington, 1988). However, the present data show that category-specific impairments can arise from pre-semantic visual deficits. For example, DW's living things impairment emerged as a direct result of his difficulties in processing the global shape of objects, and his attentional bias towards local features. Thomas et al (2002) argued that because animals tend to have the same parts (head, tail, 4 legs etc), they require more global processing than nonliving things to determine the rather subtle differences in the relative size and scaling of parts that differentiate one animal from another (see also Sacchett & Humphreys, 1993). Furthermore, fruit and vegetables often have only one 'part' and, consequently, successful recognition of these items depends on accessing information about the overall shape of the object. In contrast, nonliving things tend to have salient and characteristic parts (e.g. the dial of a telephone, the tines on a fork), and therefore, successful processing of constituent parts may be sufficient to uniquely identify many of these objects. Consistent with this idea, the present data showed that when local information was removed, in silhouettes, normal subjects found it more difficult to identify nonliving compared to living things (in Experiment 3), i.e., local information was less important for the

recognition of living things and many of these items were successfully recognised on the basis of their overall shape alone.

The data clearly challenge the assumption (sometimes explicit and sometimes implicit) that category-specific impairments *necessarily* reflect damage at a semantic level (see also, Arguin, 2002; Funnell, 2000; Riddoch & Humphreys, 1987). Interestingly, a number of the patients with category-specific impairments apparently arising from damage to a semantic system also show impairments on tests of pre-semantic visual perceptual processing. For example, the patients reported by Caramazza and Shelton (1998), Lambon-Ralph et al (1998) and Samson et al (1998) all performed poorly on tests of object decision. Object decision tasks are typically used to assess access to pre-semantic structural descriptions and do not necessarily require access to stored semantic knowledge, although semantic knowledge may facilitate object decision in normal subjects. Therefore, one could argue that patients' poor performance on object decision indicated that their access to pre-semantic structural descriptions was not fully intact, and it is possible that this impairment, rather than a semantic impairment, could account for their difficulties recognising living things. Thus, one important conclusion from the data reported in the current chapter is that future studies of patients with category-specific impairments need to provide a more detailed analysis of *perceptual,* as well as semantic, abilities and impairments.

CHAPTER 5

AN INVESTIGATION INTO CATEGORY-SPECIFIC RECOGNITION IN THE HUMAN BRAIN USING MAGNETOENCEPHALOGRAPHY (MEG)

5.1 INTRODUCTION

This chapter investigates category-specificity using the functional imaging technique magnetoencephalography (MEG). The first section reviews, in chronological order, the functional imaging literature on category-specificity. The second section introduces the theory behind MEG and gives a technical explanation of how MEG works. In the final section, experiments designed to evaluate the neural correlates of category-specific knowledge are reported. In particular, this chapter will address the two main theoretical claims concerning category-specificity. First, whether there is neural specialisation in the brain according to category (e.g. Caramazza & Shelton, 1998) or feature-type (e.g. Warrington & Shallice, 1984), and second, whether categorical knowledge is represented in a more distributed, non-differentiated system (e.g. Devlin et al, 1998). The latter theory would predict relatively equivalent cortical activity regardless of the category or semantic properties involved, whereas the former would predict the activation of distinct neural regions, differentiated by category or semantic property.

5.2 Review of functional imaging work on category-specificity

This section reviews all seventeen published studies to date (July 2002) on category-specificity that have used functional imaging techniques to measure the neural activity associated with recognising living and nonliving things. Two related electrophysiological studies are also reported. Table 5.1 shows the total (42) individual areas of the brain that have been implicated in these reports (see Glossary in Appendix B for expansion of the brain area acronyms).

Table 5.1. All seventeen functional imaging studies and two electrophysiology studies that have investigated the nature of category-specificity in the human brain.

Study	Method	Area of investigation	Paradigm	Stimuli	Categories	Areas of Activity	
						Living	Nonliving
Perani et al (1995)	PET	Whole brain	Same-different recognition	Line drawings	1. Animals 2. Manipulable objects	LFFG LLG	LIFG
Martin et al (1996)	PET	Whole brain	Picture-naming	Line-drawings and Silhouettes	1. Animals 2. Tools	LLG LITG	LMTG LIFG LPM
Damasio et al (1996)	PET	Ventral temporal cortex	Picture-naming	Line drawings	1. Animals 2. Tools	LIMTG	LPMTG
Mummery et al (1996)	PET	Whole brain	Word generation	Auditory cue	1. Animals, fruit and vegetables 2. Manipulable objects	LPTG LTOJ	RIPG BAMTG
Mummery et al (1998)	PET	Whole brain	Similarity by location	Visually presented words	1. Living 2. Nonliving	LMFG RIPG	LPMTG LPHG
			Similarity by colour	Visually presented words	1. Living 2. Nonliving	No differences	LPMTG LPHG
Cappa et al (1998)	PET	Whole brain	Semantic knowledge retrieval	Visually presented words	1. Animals 2. Tools	RMFG RFFG	LTOJ LSMG RSTG RT
[a]Grabowski et al (1998)	PET	Frontal lobe regions	Picture-naming	Line drawings	1. Animals 2. Tools	No difference	LIFG LMFG
[b]Spitzer et al (1998)	fMRI	Whole brain	Picture-naming	Colour pictures	1. Animals 2. Furniture, household items	BMFG BIFG BIPG	BMFG BIFG BIPG
[c]Moore and Price (1999)	PET	Whole brain	Picture-naming	Line drawings	1. Animals, fruits 2. Tools, vehicles	BATG RPMTG	LLG
			Word-picture matching	Visually presented words; line drawings	1. Animals, fruits 2. Tools, vehicles	[a]BATG [a]RPMTG	LLG LPMTG
Perani et al (1999)	PET	Whole brain	Picture-matching	Line drawings	1. Animals 2. Tools	LFFG LIOG	LDLPFG LITG LMTG
			Word-matching	Visually presented words	1. Animals 2. Tools	LFFG LIOG LT RSPG	LPC LMTG BLG RC LCB
[a]Thompson-Schill et al (1999)	fMRI	Ventral occipito-temporal regions	Semantic knowledge retrieval	Verbally presented questions (visual)	1. Living 2. Nonliving	BFFG	BFFG
				Verbally presented questions (nonvisual)	1. Living 2. Nonliving	BFFG	No differences
[b]Chao et al (1999)	fMRI	Whole brain	Picture-naming, matching, and viewing Reading	Photographs Words	1. Animals 2. Tools	BMOG BIOG BLFG	BMFG BMPTG BITG BSTG
Gerlach et al (1999)	PET	Whole brain	Object decision (easy)	Line drawings	1. Animals, fruit and vegetables 2. Tools, vehicles, kitchen utensils	No differences	No differences
			Object decision (hard)	Line drawings	As above	RITG LAFG	No differences
Gorno-Tempini et al (2000)	PET	Whole brain	Picture-naming	Line drawings	1. Animals 2. Objects	LEXS	LPMTG
			Reading	Written words	As above	LEXS	LPMTG
Leube et al (2001)	fMRI	Whole brain	Categorisation	Written words	1. Living 2. Nonliving	RFFG RMTG RIFG	No differences
[d]Kraut et al (2002)	fMRI	Whole brain	Category-matching	Visually presented word pairs	1. Animals 2. Fruit and vegetables 3. Tools	LIFG LPCG	No differences
Devlin et al (2002)	PET	Whole brain	Lexical decision	Visually presented words	1. Animals 2. Fruits 3. Tools 4. Vehicles	No differences	No differences

	PET		Categorisation	Visually presented words	1. Animals, fruits 2. Tools, vehicles	No differences	No differences
	fMRI		Categorisation	Visually presented words	1. Animals, fruits 2. Tools, vehicles	No differences	No differences
[a]Dehaene (1995)	ERP	Whole brain	Word categorisation	Visually presented words	Animals	LTPG	No differences
Kiefer (2001)	ERP	Whole brain	Categorisation	Colour pictures	1. Animals, plants, fruits, vegetables 2. Tools, furniture, transportation, musical instruments	BITO (N1) ROT (N400) RCP (N400) RFC (N400)	LFC (N400)
				Visually presented words	As above	ROT (N400) RCP (N400)	

[a]The comparison was made between category (living or nonliving) and a baseline condition, not between living and nonliving things directly.

[b]No group data analysed

[c]Only for black and white line drawings, activity eliminated for coloured drawings.

[d]Only between 1 and 3, no differences found between 1 and 2.

In the first published functional imaging study of category-specificity, Perani et al (1995) used PET to compare the cortical areas that were activated when normal subjects performed a same-different visual recognition task on line drawings of living things (animals) and nonliving things (manipulable objects, e.g. computer mouse, sports racket). Increased activation was found in left fusiform and left lingual gyri for animals relative to manipulable objects, and in the left inferior frontal gyrus for objects relative to animals. The authors argued that their results provided evidence for the fractionation of semantic knowledge in the brain (see Table 5.1 for the paradigm, stimuli, and object categories used in each study).

Martin et al (1996) reported similar results to Perani et al (1995). They used PET to compare the areas of the brain that were activated when normal subjects named line drawings and silhouettes depicting either living things (animals) or nonliving things (tools). They reported bilateral but greater activation in the left medial occipital region (including the left lingual gyrus) and left inferior temporal lobes for the naming of animals relative to tools, and in the left middle temporal gyrus, left inferior frontal region and left premotor regions for the naming of tools relative to animals. Martin et al reported that their finding of differential activation in the left middle temporal gyrus when naming tools was similar to areas that were activated when subjects named objects associated with actions (Wise et al, 1991; Martin et al, 1995), and activation in

the left premotor area was similar to areas activated when subjects imagined grasping objects (Decety et al, 1994). Martin et al (1996) argued that their results provided evidence for a more distributed neural network of semantic representations than the broader anatomical distinctions associated with lesion based studies (see Section 1.4.1). For instance, large areas of posterior and ventral cortex have been associated with category-specific deficits for living things, whereas more anterior and dorsal areas of cortex have been associated with difficulties recognising nonliving things (Saffran & Schwartz, 1994).

Damasio et al (1996) also used PET to examine neural activation when subjects named line drawings of animals and tools. However, on the basis of their analysis of the lesion sites of category-specific patients the authors restricted the area of interest to the ventral temporal cortex. They found that animals (relative to tools) activated left inferior middle temporal cortex (an area more anterior than that found by Martin et al, 1996), and tools (relative to animals) activated left posterior middle temporal cortex (the same area found by Martin et al). Damasio et al proposed that category-specific effects were attributable to an intermediary region of processing that links stored semantic knowledge and word form information in a bi-directional fashion (similar to the lemma level proposed by Levelt et al, 1989; see Section 5.3.2). They argued that naming living and nonliving things resulted in activation of different regions because the links differed in terms of the overall physical characteristics of the items, and also in terms fine physical characteristics and specific contextual links that allow, for example, the unique recognition of familiar people and places.

Mummery et al (1996) used PET to investigate activity when subjects generated exemplars from categories of living things (vegetables, fruit, land animals, and sea creatures), and manipulable nonliving things (tool, toys, weapons, and clothes) in a twenty-second period. For nonliving relative to living things there was increased activation in left posterior temporal areas (as found by Martin et al, 1996 and Damasio et al, 1996) and the left temporo-occipital junction. For living relative to nonliving things there was increased right inferior parietal activation and bilateral antero-medial activation in the temporal lobe; this latter area is typically determined as a lesion site associated with a deficit for living things (Gainotti et al, 1995). Interestingly, the word generation task employed by Mummery et al generated no visual area activation in

medial occipital regions for living things (relative to nonliving) as was found in the Perani et al (1995) and Martin et al (1996) studies. Mummery et al contended that this difference resulted from the use of pictorial stimuli in the former two studies. The authors interpreted their findings as evidence that differences in activation between living and nonliving categories reflected different feature weightings (sensory and functional) within a distributed semantic system (Mummery et al, 1996).

Mummery et al (1998) reported data from another PET study in which subjects made similarity judgements about the different attributes associated with living and nonliving things. Subjects were presented with triads of written object names (living or nonliving things) and had to match a target with one of two distractors based on either a perceptual attribute (colour) or an associative attribute (location). The results for nonliving relative to living things showed the same areas of activation as found in all the previously discussed PET studies, regardless of attribute type, i.e., increased activation in left posterior middle temporal cortex. Increased activation in the left parahippocampal gyrus was also found, an area that has been shown to be important for semantic retrieval (Vandenberghe et al, 1996; Ricci et al, 1999). Increased activation for living things (relative to nonliving) was found during judgements about location (left middle frontal gyrus and right inferior parietal cortex), but no difference was found during judgements about colour. The lack of differential activation for words denoting living relative to nonliving things across both judgement tasks was interpreted by Mummery et al as evidence that attribute (perceptual/associative) rather than category (living/nonliving) was more important in explaining differences in cortical activity, and they concluded that there was no specific area of the brain dedicated to the semantic processing of words from the category of living things.

Cappa et al (1998) also carried out a PET investigation into the effects of semantic category and knowledge type. Subjects were visually presented with words of living (animals) or nonliving things (tools) and required to retrieve visual and functional/associative information about each word. For example, whether an animal had a short or long tail accessed visual knowledge, whether it was native to a certain country accessed associative knowledge. Similarly, whether a tool was used in the kitchen accessed functional knowledge, whether it had a long or short handle accessed visual knowledge. Cappa and colleagues found increased activity in the left temporo-

occipital junction region for nonliving things (relative to living), irrespective of the task used (the same area activated in the 4 PET studies discussed thus far). In addition, judgements made about nonliving things also showed differential activation in left supramarginal gyrus, the right superior temporal gyrus, and the right thalamus. Living things (relative to nonliving) increased activation in the right middle frontal gyrus and the right fusiform gyrus, again irrespective of the task used. Cappa and colleagues found no interaction between task and category, furthermore the category differences observed were less prominent compared to previous PET studies. Cappa et al argued that this reflected the use of a lexical task rather than pictorial stimuli (note however that neither of the Mummery et al studies used pictorial stimuli).

Grabowski et al (1998) used PET to examine the frontal regions of the brain using the same paradigm as Damasio et al (1996). A direct comparison between activation for animals and tools was not made. For both categories relative to baseline there was extensive activation in the left inferior frontal gyrus, but for tools relative to a baseline task (orientation decisions on unfamiliar faces) increased activation was observed in the anterior region of the left prefrontal gyrus (the same area found by Martin et al, 1996), and extended into left inferior and middle frontal gyri. Grabowski et al explained this activation in the same terms as Martin et al, i.e., that increased activity in premotor regions arises because of the actions associated with tools. Again, it should be noted that no direct comparison was made between living and nonliving things in the Grabowski et al study.

Spitzer et al (1998) used fMRI to examine the effects of different categories on cortical activity during a picture-naming task. Subjects were asked to covertly name living (animals) and nonliving things (furniture). For nine of the twelve subjects the authors reported relatively small regions of activation in the middle and inferior frontal gyrus and the inferior parietal lobe for both categories, however little consistency was observed across subjects for either category. This study was not as well developed as the aforementioned PET reports; the 12 subjects were not grouped together for analysis, and the area of investigation was relatively small (2cm). Nevertheless, the authors interpreted their findings as reflecting the local organisation of semantic information in the cortex, and argued for a category-specific map-like

organisation residing in middle and inferior frontal areas, and superior and middle temporal areas (Spitzer et al, 1998).

Moore and Price (1999) reported data from a PET study using pictures of living (animals and fruits) and nonliving things (vehicles and tools). The motivation behind their study was to segregate category effects from effects that were due to differences in the visual configuration of objects. They achieved this by comparing the stimuli across four groups: 1) multicomponent living things (animals), 2) multicomponent nonliving objects (e.g. vehicles), 3) living things with simple shapes (fruit and vegetables), and 4) nonliving objects with simple shapes (e.g. tools). One group of subjects named the pictures, another made same-different judgements about whether picture-word pairs were from the same category. For multicomponent compared to simple shaped objects, the right occipitotemporal, fusiform and medial extrastriate cortices were activated. In this latter area, strongest activation was found for multicomponent nonliving objects (vehicles). In the two former areas, activity was strongest for multicomponent living things (animals) and least for simple nonliving objects (tools), and there was more activity for multicomponent nonliving compared to simple nonliving things.

Left posterior temporal cortex was differentially activated for nonliving things (relative to living), but only in the picture-word matching task. In both tasks, for nonliving things (relative to living), increased activation was observed in left medial extrastriate cortex (left lingual gyrus), an area previously associated with the reverse comparison (Perani et al, 1995; Martin et al, 1996). Left lingual gyrus activation was most prominent for vehicles relative to animals, but there was also significant activation for animals relative to fruit and vegetables. The authors argued that the findings reflected the visual configuration of the items used (vehicles being the most visually complex, fruits being the least) rather than an implicit semantic category difference. For living things (relative to nonliving) increased activation was found bilaterally in anterior temporal regions extending into the insula, and the right posterior middle temporal gyrus for both tasks, but only for black and white drawings; when appropriate colouring was added the effects were eliminated. The authors concluded that the ease with which an object can be identified (structurally and semantically) is critical in determining which areas of the brain will be active, and

therefore, category specific differences can be attributable to the different demands placed on the processing of objects (such as structural complexity) rather than implicit differences in semantic category.

Perani et al (1999) continued their earlier work in a PET study that examined activity during picture and word matching tasks. In the picture-matching task for living relative to nonliving things, increased activation was found in the left lingual, fusiform, and inferior occipital gyri. For nonliving things (relative to living) increased activity was observed in the left dorso-lateral frontal cortex and left inferior and middle temporal gyri (the latter was found in all aforementioned PET studies except Moore and Price, 1999). Many of these areas were also found in the word-matching task (left fusiform gyrus and inferior occipital gyri for animals, and left middle temporal gyrus for tools), but some areas of activation were specific to the word task (left inferior parietal and frontal regions, left cerebellum, see Table 5.1). The authors interpreted their findings as providing further evidence that semantic knowledge for living and nonliving things is represented in partially separate anatomical substrates.

Thompson-Schill et al (1999) used fMRI to examine the neural activity involved when subjects answered verbally presented questions about the visual and nonvisual attributes associated with living and nonliving things (see Cappa et al, 1998 above). The authors restricted the areas of interest to ventral occipito-temporal cortex due to a declared interest in the fusiform gyrus as a site of importance for the retrieval of visual information. Thompson-Schill and colleagues found increased activation in the fusiform gyrus when subjects answered visual questions about living and nonliving things, as well as nonvisual questions about living things, but not for nonvisual questions about nonliving things. Thompson-Schill et al argued that their findings confirmed the role played by the fusiform gyrus in retrieval of visual semantic knowledge (as previously shown by Martin et al, 1995; D'Esposito et al, 1997). The authors argued that the fusiform gyrus was associated with the retrieval of visual knowledge regardless of category, and also when living things are processed, regardless of question-type. As a result the authors proposed that their findings provided evidence against the fractionation of semantic knowledge along categorical lines and instead contended that in the fusiform gyrus they have identified an area of the brain that shows differential activity dependent on modality, i.e., the recognition

of living things depends on access to stored visual knowledge – regardless of task. Note that no direct comparison was made between living and nonliving things, only between each condition and a baseline condition consisting of digitally reversed questions designed to contain no semantic information but retain auditory stimulation.

Chao et al (1999) used fMRI to examine neural activity for living (animals) and nonliving (tools and houses) things during picture naming, picture matching, picture viewing and reading object names. For pictures of tools (relative to animals) increased activation was found bilaterally in the medial fusiform gyrus and the lateral middle posterior temporal gyrus (for all subjects in all pictorial tasks). Similarly, for the reading task, there was consistent activation in the left posterior middle temporal gyrus for tools relative to animals. For pictures of animals (relative to tools) increased activation was observed in bilateral medial and inferior occipital, ventral temporal and superior temporal cortices (for all pictorial tasks). In contrast, there was no activity in the medial occipital gyrus during the reading task, and all the other regions of activity found during the pictorial tasks were inconsistently replicated across subjects. For example, 2/8 and 3/8 subjects showed significant activity in the left and right inferior occipital gyrus, respectively. Similarly, 4/8 and 5/8 subjects showed significant activity in the left and right lateral fusiform gyrus, respectively.

These latter findings are illustrative of the problems with the Chao et al study. No group analysis was carried out and an effect was deemed to be significant if a proportion of the individual subject analyses was at $p<0.05$ (a low threshold that was uncorrected for multiple comparison). Furthermore, object variables that previous studies (e.g. Moore & Price, 1999) have shown to be important such as visual complexity and name frequency were not reported. Nevertheless, the reported areas of differential activation show striking similarities to those previously reported. In particular, activity in left posterior middle temporal cortex was found in both pictorial and lexical tasks for tools (relative to animals), and the fusiform gyrus was implicated in all tasks for animals (relative to tools).

Gerlach et al (1999) used PET to examine cortical activity during an object-decision task. Subjects were required to judge whether line drawings depicted real objects or non-objects. The real objects were either living or nonliving and the task differed in

difficulty in the amount of perceptual differentiation needed to perform it, i.e., a non-object using novel parts constituted an easy decision, one using the component parts of the real objects constituted a difficult decision. When task difficulty was easy no category differences were found, however, as task difficulty increased a differential increase in activation for living compared to nonliving things was found in the right inferior temporal and anterior fusiform gyri. The authors interpreted this finding as reflecting the greater perceptual differentiation required for recognising living compared to nonliving things, and argued that category effects can arise at a pre-semantic level distinct from semantic processing (see Section 1.3.5).

Gorno-Tempini et al (2000) used PET to investigate the differences in cortical activity between six categories of pictorial stimuli (animals, objects, body parts, colours, famous faces, and maps). The authors designed a naming and a reading condition by presenting the stimuli with the written name of the picture as well (the reading condition) or without it (the naming condition). The aim of their study was to investigate whether categorical differences were dependent upon the demands placed on lexical retrieval. No category-specific effects were observed for naming relative to reading, but they were when naming and reading were considered together. For example, the commonly reported activation of the left posterior middle temporal regions was found for object and body part categories relative to the other four categories. Increased activation was found in the left extrastriate visual cortex for animals, faces and maps (relative to objects and body parts), a finding the authors suggested was due to the greater visual complexity of the former categories. Gorno-Tempini and colleagues concluded that category-specific differences in cortical activity depended on the demands placed on the processing of objects at the perceptual and semantic levels, more than the lexical retrieval level.

Leube et al (2001) used fMRI to examine neural activity while words were presented to subjects who were required to categorise items as either living or nonliving things. Increased activation was observed for living things (relative to nonliving) in right fusiform gyrus, middle temporal and inferior frontal regions. No significant difference in activation was observed for nonliving relative to living things. Leube et al argued that the right hemisphere regions activated in their study for living things are in line with areas of damage typically found in patients with category-specific deficits for

living things (see Section 1.4.1), and furthermore, that these different areas are representative of a distributed model of semantic memory such as the OUCH (Caramazza & Shelton, 1998 see Section 2.1). The right hemispheric activations during processing of the living category in this study are at variance with results from aforementioned PET studies that found predominantly left hemispheric activation (e.g. Damasio et al, 1996 and Martin et al, 1996). These PET studies examined lexical retrieval in a naming task of pictorially presented animals and tools. Leube and colleagues argued that it was likely that naming animals and answering questions about their properties is cognitively different from a living-nonliving categorisation task which focuses much more on features of the objects that are critical for distinguishing among these categories, i.e., features that define the living category.

Kraut et al (2002) used fMRI to investigate cortical activity during a task where subjects decided whether pairs of presented words were members of the same category (animals, tools, fruit and vegetables). The authors found no areas that were specifically activated for any one of the three categories. However, increased activation was observed for pairs of tools and pairs of fruit and vegetables (relative to pairs of animals) in the left BA6/44 junction (inferior frontal/precentral gyri). The lack of activation for animals suggested that the left BA6/44 junction is involved in an operation common to tools and fruit and vegetables. Kraut et al suggested that this operation could be related to the movement patterns associated with both categories, i.e., a salient feature of both tools and fruit and vegetables is that they can be manipulated by hand (e.g. a screwdriver is held and twisted, an orange is held and peeled), whereas for animals the features are not as prominent. As a result, Kraut et al (2002) argued that the left BA6/44 area of cortex was organised in a feature-specific rather than a category-specific manner.

Devlin et al (2002) investigated the neural correlates of subject's semantic knowledge about different categories using both PET and fMRI. They conducted three experiments; in the first they used PET to examine the cortical activity associated with making lexical decisions (deciding whether a visually presented word was real or not) about items from four categories (animals, fruit, tools, and vehicles). The authors found no significant differences between any of the four categories or between living and nonliving things grouped together. Devlin et al carried out a second PET

experiment using a categorisation paradigm (living-nonliving) to increase the demands on the semantic system (the lexical task required activation of semantic and phonological regions whereas the categorisation task required only semantic activation). Again, no significant effects between living and nonliving things were observed. It should be noted that, in contrast to the majority of functional imaging studies reported here, Devlin et al corrected for multiple comparisons at a statistical threshold of $p<0.05$

In a third experiment Devlin et al replicated the categorisation experiment, this time using fMRI to increase the spatial resolution. They contended that the lack of effects found in the second experiment could have been due to PET having insufficient spatial resolution to differentiate functional differences between proximal neural regions. However, no significant differences in activation were found when subjects categorised living and nonliving things. The authors concluded that their data provided evidence that semantic knowledge is represented in a distributed neural system, undifferentiated by category or feature-type, as opposed to being segregated in neural systems dedicated to different domains.

In addition to the functional imaging work two electrophysiological studies have examined the nature of category-specificity. Event-related potentials (ERPs) have been successfully applied to examine perceptual and semantic processes in object categorisation. For instance, Tanaka et al (1999) observed that subordinate categorisations (e.g. Siamese) of a depicted object elicited a larger N1 component (the N1 component is an early negative deflection that reflects perceptual processing (Mangun & Hillyard, 1991)) than basic level (e.g. cat) or superordinate categorisations (e.g. animal) starting at about 150ms after target presentation. The N400 component, a negative deflection at about 400ms, has been shown to be sensitive to semantic processing deviations in, for example, differences between concrete and abstract words (Kounios & Holcomb, 1994), as well as superordinate relative to basic level categorisation (Tanaka et al, 1999). Dehaene (1995) investigated the time course of visual word processing, using ERPs. He employed a word classification task using stimuli from each of the following categories: Animals, action verbs, names of famous people, numerals, and consonant strings. Results showed increased activity over left temporo-parietal regions for animals, over left

inferior temporal regions for proper names, and bilaterally over the same latter region for numerals. Dehaene (1995) argued that these results showed a coarse localisation of the different activity involved in processing words from different categories, however, no direct comparison between living and nonliving things was made.

Kiefer (2001) carried out an ERP study, in which, subjects were required to judge whether a superordinate category probe (presented verbally or by means of two pictures from the chosen category) was appropriate to a target stimulus (presented either as a name or a picture). Kiefer found that early ERP differences emerged for living and nonliving targets (between 160-200ms), whereby living things elicited a greater N1 ERP component than nonliving things, an effect that was restricted to pictorial targets (the N1 component is an early negative deflection that reflects perceptual processing and is enhanced when attention is directed to visual stimuli (Mangun & Hillyard, 1991)). These early effects can be interpreted as reflecting visual perceptual processing. For example, Tanaka et al (1999) found that more complex perceptual processing of subordinate categorisations (e.g. a poodle) compared to superordinate categorisations (e.g. an animal) elicited greater N1 amplitudes. Kiefer proposed that it was the perceptual similarity of living things that accounted for category effect observed in the early ERP (see Humphreys et al, 1988). Later ERP's (300-500ms) also showed category effects, with living things eliciting a less negative potential bilaterally over occipito-temporal regions and nonliving things less negative over left fronto-central regions. These late ERP effects were found for both word and pictorial stimuli, and are consistent with living and nonliving things reflecting differences at a semantic level of representation perhaps in terms of functional-associative information. Hence, Kiefer's findings suggest that perceptual as well as semantic sources contributed to category-specific effects, and he concluded that they support the view that semantic knowledge associated with different categories is represented in multiple subsystems that are similarly accessed by pictures and words (Kiefer, 2001).

In summary, the functional imaging studies of category-specificity produced a diverse set of findings (see Tables 5.2 to 5.5). There has been very little between-study consensus concerning the cortical areas involved: In the sixteen studies discussed that made direct living-nonliving comparisons there were 42 different areas of cortex

implicated (22 for living; 20 for nonliving). The two most consistent findings were activation of the left middle temporal gyrus (7 out of 16 studies) and activation of left inferior frontal gyrus (4 out of 16 studies) for nonliving relative to living things. The functional significance of these areas may be that because function and associated action are important defining features for nonliving things (see the results from Section 2.2.2) the areas of the brain associated with these properties are differentially activated for nonliving compared to living things. Evidence supporting this idea comes from studies that found similar areas of activation when subjects named objects associated with actions (Wise et al, 1991; Martin et al, 1995).

Interestingly, both behavioural (Tucker & Ellis, 2004) and functional imaging (Chao & Martin, 2000; Grezes & Decety, 2002) studies have proposed that viewing tools automatically activates motor representations. This would suggest that simply viewing a nonliving object such as a tool is sufficient to generate activation with respect to potential action. Some evidence related to this latter finding comes from a series of experiments by Rizzolatti and colleagues (diPellegrino et al, 1992; Gallese et al, 1996; Rizzolatti et al, 1998), who discovered that a particular set of 'mirror neurons' in the monkey premotor cortex (area F5) were activated both when the animal performed a grasping action, and when it observed a conspecific perform the same action. A number of studies have shown evidence for the same mirror-matching system for action execution and observation in humans (Buccino et al, 2001; Fadiga et al, 1995; Hari et al, 1998). Therefore, it is possible that a mirror-matching mechanism could be activated when viewing particular objects that have potential action associated with them.

On the whole, consistencies in brain areas for imaging studies of category-specificity were limited, and as outlined in Tables 5.3 to 5.6, they were often observed in studies that employed different paradigms and/or used different stimuli. Moreover, the same areas of cortex have been implicated for both categories in different studies. For instance, the left lingual gyrus was reported as being differentially active for living things (relative to nonliving) in two studies (Perani et al, 1995; Martin et al, 1996), and for nonliving things (relative to living) in a further two studies (Moore & Price, 1999; Perani et al, 1999).

Table 5.2 Consistency of activated brain areas for pictures of living things

Task	Stimuli	Area of activation	No. of studies that found activation here
Picture-naming	Line drawings	1. LLG	1/7
	Line drawings	2. LITG	1/7
	Line drawings	3. LIMTG	1/7
	Line drawings	4. BATG	1/7
	Line drawings	5. RPMTG	1/7
	Line drawings	6. LFFG	1/7
	Line drawings	7. LIOG	2/7
	Photographs	8. BMOG	1/7
	Photographs	9. BIOG	1/7
	Photographs	10. BLFG	1/7
	Line drawings	11. LEXS	1/7
	Colour drawings	12. BMFG	1/7
	Colour drawings	13. BIFG	1/7
	Colour drawings	14. BIPG	1/7
Semantic tasks			
Picture-word matching	Line drawings; visually presented words	1. BATG	1/1
		2. RPMTG	1/1
Pre-semantic tasks			
Object decision	Line drawings	1. RITG	1/1
		2. LAFG	1/1
Same-different judgements	Line drawings	1. LFFG	1/1
		2. LLG	1/1

Table 5.3 Consistency of activated areas for pictures of nonliving things

Task	Stimuli	Area of activation	No. of studies that found activation here
Picture-naming	Line drawings	1. LMTG	2/7
	Line drawings	2. LIFG	2/7
	Line drawings	3. LPM	1/7
	Line drawings	4. LPMTG	2/7
	Line drawings	5. LLG	1/7
	Line drawings	6. LDLPFG	1/7
	Line drawings	7. LITG	1/7
	Photographs	8. BMFG	2/7
	Photographs	9. BMPTG	1/7
	Photographs	10. BITG	1/7
	Photographs	11. BSTG	1/7
	Colour drawings	12. BIFG	1/7
	Colour drawings	13. BIPG	1/7
Semantic tasks			
Picture-word matching	Line drawings; visually presented words	1. LLG	1/1
		2. LPMTG	1/1
Pre-semantic tasks			
Same-different judgement	Line drawings	1. LIFG	1/1

Table 5.4 Consistency of activated areas for words of living things

Task	Stimuli	Area of activation	No. of studies that found activation here
Semantic tasks			
Word generation	Auditory cue	1. LPTG	1/1
		2. LTOJ	1/1
Categorisation	Visually presented words	1. RFFG	1/3
		2. RMTG	1/3
		3. RIFG	1/3
Category-matching	Visually presented words	1. LIFG	1/1
		2. LPCG	1/1
Word-matching	Visually presented words	1. LFFG	1/1
		2. LIOG	1/1
		3. LT	1/1
		4. RSPG	1/1
Semantic knowledge retrieval	Visually presented words	1. RMFG	1/1
		2. RFFG	1/1
Pre-semantic tasks			
Similarity by location	Visually presented words	1. LMFG	1/1
		2. RIPG	1/1

Table 5.5 Consistency of activated areas for words of nonliving things

Task	Stimuli	Area of activation	No. of studies that found activation here
Semantic tasks			
Word generation	Auditory cue	1. RIPG	1/1
		2. BAMTG	1/1
Word-matching	Visually presented words	1. LPC	1/1
		2. LMTG	1/1
		3. BLG	1/1
		4. RC	1/1
		5. LCB	1/1
Semantic knowledge retrieval	Visually presented words	1. LTOJ	1/1
		2. LSMG	1/1
		3. RSTG	1/1
		4. RT	1/1
Pre-semantic tasks			
Similarity by location	Visually presented words	1. LPMTG	1/1
		2. LPHG	1/1
Similarity by colour	Visually presented words	1. LPMTG	1/1
		2. LPHG	1/1

5.2.1 Methodological issues

It is clear that methodological differences are important in explaining the between-studies variability. In a review of the functional imaging literature on category-specificity, Price and Friston (2002) proposed that between-study inconsistencies were due to the different tasks and stimuli employed, i.e., category effects were context dependent. The authors proposed that one area that was implicated in one study might not be in another study if the task or stimuli were different because specific activity in a single cortical area was dependent upon all the regions that provided afferents to that area.

In the sixteen studies discussed a range of paradigms were used to examine the difference between living and nonliving things (see Table 5.1). This is problematic because there are important differences in the cognitive demands of the tasks. For example, picture naming involves a number of stages (e.g. visual processing, semantic processing, phonological retrieval, see Glaser et al, 1992), and even if consistent differences were found between living and nonliving things it would not be clear where the differences emerged (e.g. at perceptual, semantic or lexical levels). On the other hand, in a living-nonliving semantic categorisation task it is not necessary to

encode phonological information from semantics about the names of the object. Thus, the lack of consistency across studies could occur because some tasks tap the level at which living and nonliving things are differentiated and some do not. Another methodological difference was the stimuli used (pictures, words, or both pictures and words). However, the consistency of activated brain areas did not improve when studies using the same stimulus type were considered (see Tables 5.3 to 5.6). Furthermore, a number of studies (see Section 1.3.1) have demonstrated that category-specific effects can arise spuriously due to differences in uncontrolled stimulus factors such as familiarity, visual complexity, and structural similarity.

Another important feature that contributed to the divergent claims of the functional imaging studies was a variation in the threshold of the selected level of statistical significance. In many of the early PET studies reported in this section an uncorrected significance level of $p<0.001$ was employed, however, because of the large amount of comparisons made (a typical PET study analyses around 200,000 voxels, resulting in approximately 500 independent observations (Devlin et al, 2002)) it is now almost standard practice to use a corrected probability level to avoid false positives (Worsley et al, 1996). Therefore, while some of the later studies discussed in this section (e.g. Devlin et al, 2002) formally corrected their statistical maps to account for multiple comparisons, many of the earlier reports employed less conservative thresholds (e.g. Martin et al, 1996), and as a result may have erroneously reported areas of differential activation between living and nonliving things.

The present chapter used MEG to examine the differences between living and nonliving things in the human brain. As previously mentioned, the majority of the functional imaging work on category-specificity has been carried out using PET and fMRI techniques. Therefore, in addition to providing evidence for which areas of the brain are involved in the recognition of living and nonliving things, and assessing the implications for the discussed functional models of category-specificity, this chapter utilised a new method of measurement and analysis for the investigation of category-specific effects (see Section 5.4.4).

5.3 Magnetoencephalography (MEG): A theoretical and technical explanation

Magnetoencephalography (MEG) is the measurement of magnetic fields generated by intercellular electric currents in the brain (see Figure 5.1). Measurement of these fields close to the surface of the head allows localisation of the origin of the electric currents and can be used to map cortical brain function. MEG is closely related to electroencephalography (EEG) in that both methods measure signals generated by homogenous synchronised neuronal activity in the brain, and have equivalent temporal resolution (millisecond by millisecond). As the electrical events of single neurons typically last from one to several tens of milliseconds, both techniques can follow the rapid changes in cortical activity that reflect ongoing signal processing in the brain. Theoretically, MEG and EEG differ in a number of ways: First, a sensory stimulus that activates an area of the cortex is associated with a primary current source related to the movement of ions due to their chemical concentration gradients (Hamalainen et al, 1995). The electrical potentials detected by EEG represent what are known as volume currents in the surrounding medium of nerve cells. The corresponding magnetic field is generated by both the primary and volume currents, and is orthogonal to the electrical potentials. MEG therefore detects the magnetic field produced by the postsynaptic dentritic potentials of pyramidal cells within the cortex (Williamson & Kaufman, 1989).

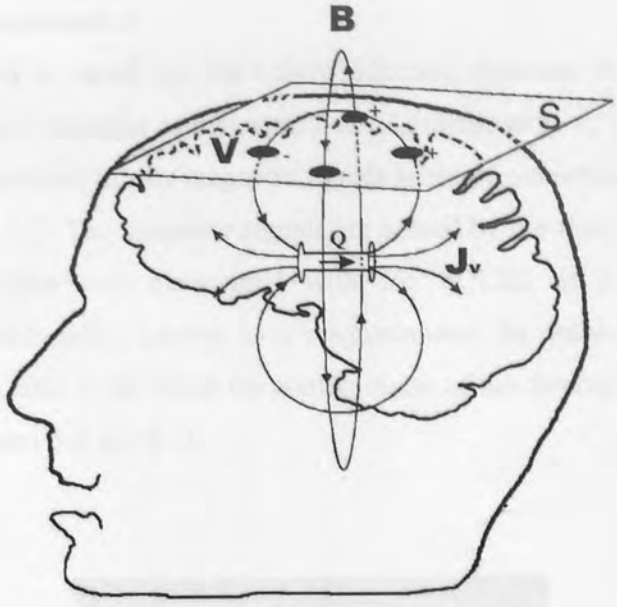


Figure 5.1. The relationship between the magnetic fields outside the head and the electrical currents in the brain is shown. A current source with strength Q causes a current flow Jv within the brain. This current flow causes a potential difference V on the scalp (measured with EEG) and a magnetic field B outside the head (measured with MEG). (Source: Aston University, Neurosciences Research Institute (NRI), MEG website).

Another theoretical difference concerns the components of the signal measured. EEG records both radial and tangential components of a signal, while MEG only records tangential sources. This is because in certain finite conductor geometries the volume current causes an equal but opposite field to that generated by the primary current (Hamalainen et al, 1993). Therefore, the external field is cancelled out and hence MEG predominantly measures activity from the fissures of the cortex. Fortunately, this restriction is not as problematic as it may first appear because all primary sensory areas of the brain (visual, auditory and somatosensory) are contained in the fissures and are therefore subject to detection by MEG. Moreover, the source of the signals from the gyri of the human brain can be adequately detected because the gyri are rarely exactly tangential to the scalp.

5.3.1 MEG instrumentation

The MEG method is based on the superconducting quantum interference device (SQUID), a sensitive detector of magnetic flux (Zimmerman et al, 1970). The device enables the measurement of tiny magnetic signals arising from neuronal activity in the brain (see Figure 5.2). The magnetic signals are sensed by the flux transformer in the form of a detection coil maintained with the SQUID at a superconducting temperature, a combination known as a magnetometer. In order to cancel out the massive magnetic field of the Earth the configuration of the detection coil needs to be modified (see figures 5.3 and 5.4).

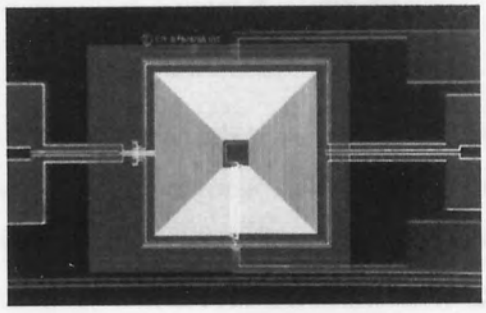


Figure 5.2. A SQUID is shown. The SQUIDS sensor and flux transformer coupling coils and feedback coils are fully integrated into this planar design. From the coupling coil, superconducting leads are brought out to tabs for inter-connection to the pickup coil of each MEG detector. (Source: CTF Inc. website)

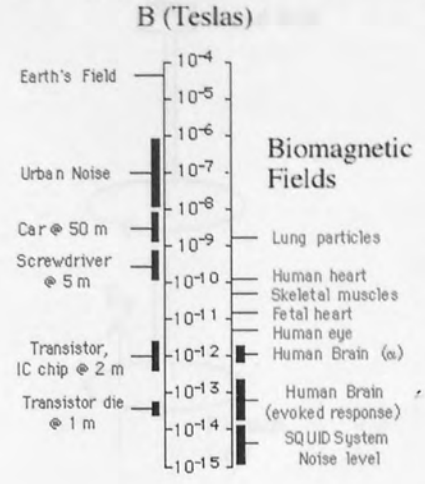


Figure 5.3. This figure shows the strength of the magnetic fields produced by sources in the brain with respect to magnetic fields produced by other sources in the body and by environmental sources. The magnetic fields of interest in this chapter are 100 million times smaller than the earth's magnetic field and one million times smaller than the magnetic fields produced in an urban environment. (Source: CTF Inc. website)

The coil is replaced by a form of winding arranged to give two coils in opposite directions; a configuration that forms a device called a gradiometer. This gradiometer is sensitive to nearby magnetic currents affecting only one coil but not to distant currents affecting both coils equally, thereby allowing minute magnetic signals such as those emanating from the brain to be measured, whilst cancelling out the Earth's massive magnetic field. Cohen (1972) carried out the first SQUID measurement. He measured spontaneous α activity in a healthy subject and the abnormal brain activity of an epileptic patient. It was this pioneering work that led to the development of MEG.

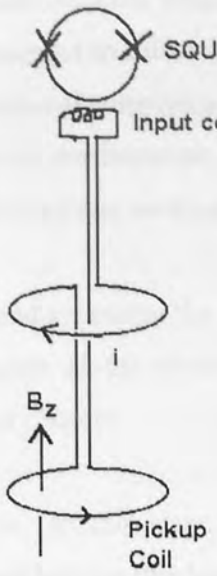


Figure 5.4. A schematic of a first order axial gradiometer is shown, consisting of two oppositely wound coils inductively coupled to the SQUID sensor. (Source: Aston University, NRI, MEG website).

Once the magnetic field is measured the source of the MEG fields needs to be calculated. Von Helmholtz (1853) showed that deducing the source currents responsible of the externally measured field has no unique solution because a number of different current distributions within the head could explain the measured brain activity – a concern known as the electromagnetic inverse problem. There are a number of modelling techniques available that address this problem by constraining the spatial extent of the sources. One such source modelling technique involves restricting the solution to a single equivalent current dipole (ECD), which approximates the flow of electrical current in a constrained spatial area, thereby reducing the problem to something more tractable.

5.3.2 MEG as a method of study for category-specificity

Although there have been many functional imaging studies of category-specificity (see Section 5.2), none of these used MEG. However, two studies by the same group of researchers have used MEG to look at the processes involved in picture naming (Levelt et al, 1998; Salmelin et al, 1994). Salmelin et al (1994) demonstrated that the dynamics of cortical activation related to the time course of the stages in picture

naming progressed bilaterally from occipital visual cortex toward temporal and frontal regions. Levelt et al (1998) attempted to relate the observed cortical activation from Salmelin et al's study to the functional components of the picture naming process, and on the basis of a meta-analysis of the literature Levelt and colleagues proposed the following temporal stage model of picture naming (see Levelt et al, 1991):

0-150msec: Visual processing and accessing the lexical concept. This stage involves computing a visual representation of the object from the visual image, and then activating the appropriate lexical concept.

150-275msec: Lemma selection. At this stage the lexical concept spreads to the corresponding word in the mental lexicon (the lemma).

275-400msec: Phonological encoding: At this stage the lemma spreads to the corresponding word form representation (the morpheme), which represents the phonemes, syllables and metrical structure of the selected word, known as the phonological shape.

400-600msec: Phonetic and articulatory processing. At this stage the word's articulation is initiated and implemented.

Levelt et al (1998) used MEG to investigate the time course of picture naming by localising the active cortical areas during each successive stage of processing. They modelled the data obtained from MEG using eight equivalent current dipoles (ECDs). Levelt et al reported that a large number of dipoles were fitted for each of their eight subjects, however, consistency in location across subjects was not often found. For example, in the stage of visual processing and accessing the lexical concept they found two or three sources per subject in the occipital cortex (however they omitted to report the areas involved due to a declared disinterest in early visual processing). For lemma selection there were large numbers of variable sources modelled throughout occipital, parietal and temporal regions, but the most reliable source (for seven out of eight subjects) was found in the right parietal cortex along the posterior of the superior temporal sulcus. For phonological encoding, dipoles were fitted (for six out of eight subjects) in left posterior temporal gyrus and the temporo-parietal junction

(consistent with Wernicke's area). Finally, a number of dipoles were found in the phonetic and articulatory processing stage, primarily in sensory-motor cortex, but these were not reliable across subjects.

Although Levelt et al (1998) reported some interesting findings concerning the time-course and location of successfully fitted dipoles the majority of their between-subjects findings were inconsistent. One reason for this inconsistency may be the choice of analysis: Dipole source modelling has been successfully employed in conventional evoked-potential experiments in which hundreds of brief epochs are averaged to form a phase-locked response, but cognitive tasks such as picture naming may be inherently difficult to model because the data is non-phase-locked to the stimulus and, as is shown in the following sections, large discrete areas of cortex may be involved. Moreover, not all the literature agrees with Levelt et al concerning the proposed timings of their model. For instance, as outlined in Section 5.2, Kiefer (2001) found late ERP effects (300-500ms) that were consistent with processing at a semantic level of representation.

5.3.3 Overview of proposed experiments

The purpose of the experiments reported in this chapter was to investigate the neural correlates of different categories of knowledge; and here for the first time MEG is used to evaluate whether there are category-specific brain areas. The first experiment used an overt picture-naming paradigm to determine whether there were cortical regions selectively activated by specific categories of object (living and nonliving things). The second experiment replicated the first, this time using a covert picture-naming paradigm to ensure response accuracy and alleviate any possible facial movement artefacts associated with overt naming. The third experiment used a categorisation task, again to determine whether there were brain regions selectively activated by living and nonliving things. In addition, this latter experiment also tested for any differences between the tasks of naming and superordinate categorisation. For example, in the majority of studies reported on category-specificity the inferences concerning the existence of neural regions specific to encoding knowledge for different categories of items are drawn from picture naming tasks using stimuli from different target categories. Therefore, the naming task itself does not explicitly assess the categories of these items. Typically, in discrete models of object naming (see e.g.

Glaser, 1994) it is assumed that naming and categorising activate the same perceptual components. In addition, naming and superordinate categorisation both activate semantic features, although naming requires computation of more semantic features than categorising for identification. Therefore, the tasks differ in that categorising does not require access to the names of objects. Hence, if category differences emerged at perceptual levels both tasks should find them. At semantic levels both tasks should find category differences but more so for object naming, and if category differences emerged at a lexical level they should only be found in the naming task. Accordingly, in the third experiment reported in this chapter an explicit item categorisation task (living-nonliving) was employed to investigate these predictions.

Experiments 4 and 5 used the same covert naming and categorisation tasks as experiments 2 and 3, respectively, but this time living and nonliving items were controlled for their level of visual complexity. These latter experiments were designed to assess the hypothesis that category-specific effects can arise for living things due to the increased perceptual demands they place on the (pre-semantic) system due to their structural similarity compared to nonliving things (e.g. Humphreys et al, 1988; Tranel et al, 1997; see Section 1.3.5). Therefore, the aim of the five experiments in this chapter was to assess the predictions made by the theories of category-specificity outlined in Section 1.3.

1) Caramazza and Shelton (1998) predicted a tripartite division between animals, plants and tools at multiple processing levels (perceptual, semantic, lexical). No predictions were made about possible sites of activation.

2) The sensory-functional hypothesis (e.g. Warrington and Shallice, 1984) predicted a difference between living and nonliving things in terms of sensory and functional knowledge. Activation was predicted to be in sensory areas for living things and motor areas for nonliving things, and that category effects would be observed in both object naming and superordinate categorisation.

3) Moss and colleagues (see e.g. Moss et al, 1997) predicted a neuroanatomical difference between living and nonliving things, but only for basic level naming, not superordinate categorisation. They proposed that this difference would be in anterior

temporal cortex, because basic level naming of living things requires greater differentiation than categorisation (and this area has been shown to be involved in visual differentiation, see e.g. Moore & Price, 1999).

4) Humphreys and Forde (2001) predicted a neuroanatomical difference between living and nonliving things, but in more posterior regions than proposed by Moss and colleagues, because living things require more 're-activation' of areas involved in early visual processing. They predicted that differences between living and nonliving things would be greater in basic level naming compared to categorisation because less reactivation is required for superordinate categorisation.

5.4 EXPERIMENTAL INVESTIGATIONS

5.4.1 Method

In all five experiments, eight right-handed subjects with normal vision and no known psychiatric or neurological illnesses participated. Each subject had a structural (T1-weighted) MRI scan in order to map activity onto individual sulci/gyri configurations. Subjects were seated in a CTF Inc. 151-channel whole-head MEG system (see Figure 5.5) employing 151 super-conducting SQUID sensors arranged in a helmet array. The head was fixed using an inflatable cuff between the head and the helmet. Co-registration with MRI was obtained by a surface matching procedure. Three small reference coils positioned over bony landmarks on the head (the inion and pre-auricular notches) were localized by the CTF system software pre- and post- data acquisition. On completion of an experiment a Polhemus 3D digitiser was used to localise the coils and digitise the subject's head shape. Using a surface matching procedure between the MRI head surface and the digitised head surface, an accurate co-registration of the MEG data and the MRI was made. Visual stimuli generated with a VSG visual stimulator (CRS Ltd) were presented on a calibrated RGB monitor (Eizo T-1520) viewed via a mirror through a window in a magnetically shielded room, such that the stimulus subtended approximately 2x4 degrees of visual angle. The VSG produced timing triggers synchronous with the onset of stimuli, which were recorded by the MEG data acquisition system.

Figure 5.5. The CTF Inc. 151-channel whole-head MEG system at the Wellcome Trust Laboratory for MEG studies, Aston University.

5.4.2 Data analysis

In the first experiment, two methods were applied to the data: Source localisation by dipole modelling was used to provide detailed information concerning the temporal sequence of cortical activation. Group-SAM (Synthetic Aperture Magnetometry) was used to identify the areas of maximum change in cortical synchrony between two (active and passive) conditions.

5.4.3 Dipole source localisation

The evoked magnetic signals, synchronised to stimulus onsets, were averaged within each condition, individually for each subject. Characteristic changes in the MEG response between different conditions were identified and the anatomical localisation

of active brain sources estimated with single equivalent current dipole models using least-squares minimisation within a homogeneous spherical head model. The time-course of activity of each modelled source was determined using a Chi-squared goodness-of-fit measure of the dipole model to the acquired response. Monte-Carlo simulations were also performed to establish confidence volumes of the localisation of dipoles.

5.4.4 Group-SAM (Synthetic Aperture Magnetometry)

SAM is a synthetic beamformer method for the analysis of MEG data (Robinson & Vrba, 1999; Seikihara et al, 2002; Singh et al, 2002; Van Veen et al, 1997) in which changes in correlated activity across the MEG sensors are detected between a control state and an active state. SAM has been previously used in studies of motor cortex (Taniguchi et al, 2000), sensory cortex (Barnes et al, 2001), midline theta rhythms (Ishii et al, 1999), verbal fluency and biological motion (Singh et al, 2002). A limitation of adaptive beam-former techniques is that perfectly synchronous sources of activity cancel each other out and are therefore difficult to detect by the beam-former. This causes problems analysing data from experiments that examine source activity by means of averaging over hundreds of brief epochs to form a phase-locked response. The shorter the epoch, the greater the probability of finding highly correlated time-course activity from multiple sources. However, the two sources would have to maintain perfect synchrony over the entire course of the experiment to be invisible, and it has been shown that two sources can be resolved at relatively large temporal correlation levels (Van Veen et al, 1997). Hence, SAM is particularly suitable for analysing non-phase-locked data over relatively long epochs because the probability that multiple sources of activity can remain temporally synchronised over epochs of a second and above is low. Therefore, SAM has advantages over dipole modelling in MEG research because it allows complex cognitive processes that activate numerous brain regions, which may not be tightly phase-locked to the onset of a stimulus, to be investigated.

In SAM, each voxel in the brain is linked to the detection array using an optimal spatial filter for that voxel. The MEG data is then projected through this spatial filter to give a measure of current density, as a function of time, in the target voxel. As this voxel time-series is calculated using a weighted sum of the MEG sensors, it has the

same millisecond time resolution as the original MEG signals. If this time-series is then divided into active and passive states, Fourier analysis can be used to calculate the total amount of power in each frequency band, within each of the active and passive blocks. These active and passive states can be several seconds long, allowing MEG task designs that are identical to those used in fMRI studies (Singh et al, 2002). The difference between these spectral power estimates for the active and passive states can then be assessed using a t-statistic calculated over all such blocks. This procedure can be repeated voxel-wise over the whole brain to generate a three-dimensional image of differential cortical activity. Note that by estimating the spectral power using all the time-points within an active or passive block, temporal resolution is relinquished in order to increase both frequency resolution and the signal-to-noise ratio.

The suitability of SAM for measuring changes in cortical power during cognitive tasks coincides with recent interest in the literature in frequency-specific focal changes in cortical oscillatory power during task-related sensory, motor, and cognitive tasks. In particular, Pfurtscheller and Lopes da Silva (1999) described changes of oscillatory activity as either time- and phase-locked (evoked), i.e., an Event-Related Potential (ERP), or as only time-locked (induced), i.e., Event-Related Synchronisation (ERS) or Event-Related Desynchronisation (ERD). ERS represents a localised amplitude increase of oscillatory activity, and ERD a localised amplitude decrease of oscillatory activity, during the active relative to the control state. For instance, a characteristic example of ERD is the blocking of occipital alpha rhythm after visual stimulation (Pfurtscheller, 1992), whereas an example of ERS is the inducement of gamma activity during visual processing (Singer, 1993).

In the experiments presented in this chapter SAM images were constructed on a 5x5x5mm grid throughout the whole brain. Power changes, interpreted as ERS or ERD between the passive and active epochs, were calculated in the following frequency bands: 5-15Hz, 10-20Hz, 15-25Hz, 20-30Hz, 25-35Hz, and 30-40Hz. These frequency bands were selected because, to date, there have not been any reported studies investigating the role of different frequencies for naming and categorising visually presented items. Therefore, a wide range of frequency bands were selected to cover many of the natural frequencies of the brain that have been

associated with functional aspects of different cognitive processing tasks. For example, alpha activity (8-13Hz), traditionally considered as the spontaneous or 'idling' rhythm of the brain, has been shown to be functionally important for sensory, motor, and cognitive processes (see Kolev et al, 2001 for a review). Beta activity (13-30Hz) has been particularly associated with motor brain function. For instance, increased beta activity has been found to correlate with the preparation and execution of movements (Pfurtscheller et al, 1998). Even action observation has been shown to attenuate beta activity (Hari et al, 1998). There has also been some recent evidence for the functional role of gamma oscillations (>30Hz) in cognitive tasks involving perception. In particular, one influential theory is that synchronised neuronal activity in the gamma-band may reflect the synchronisation of localised neuronal populations, and could be viewed as a candidate for understanding 'neuronal binding', i.e., how distributed brain activities are integrated during specific processing such as object representation (Tallon-Baudry & Bertrand, 1999).

Each subject's anatomical MRI was re-sliced in the same orientation and position as the SAM functional volume. Using SPM99 (Friston et al, 1995), this re-sliced volume was spatially normalised into the same standard template space as the fMRI datasets. The non-linear transformation matrix that is necessary to perform this normalisation was then applied to each of the functional SAM volumes, in each frequency band, and for each subject. Hence, all of the 48 SAM images (eight subjects, six frequency bands) were then in the same three-dimensional co-ordinate space, and appropriate for use in a group statistical analysis using a non-parametric permutation toolbox for SPM called SnPM (this method of analysis only became available in early 2002) (Nichols & Holmes, 2002). Within SnPM, analysis was performed using a multiple-subject single-condition design, i.e., for eight subjects, 128 permutations were carried out.

There are two levels of inference available within SnPM: voxel-level inference, which looks for those voxels that are significantly activated at the $p<0.05$ level (corrected for multiple comparisons); and cluster-level inference, which assesses whether the size of a cluster is significantly large at the $p<0.05$ level. This second inferential method takes into account that a large area of relatively high t-statistics clustered together can be significant even if the individual voxels within that cluster do not reach

significance at the voxel-level of inference. The results were visualised using both SPM and mri3dx on a template brain. Cluster sizes and positions were determined automatically using mri3dX and data from the Talairach Daemon database (Lancaster et al, 2000). Where cluster co-ordinates are given, they are expressed in the Montreal Neurological Institute (MNI) version of the bicommissural co-ordinate system.

5.5 Experiment 1: Naming (overtly) living and nonliving things

5.5.1 Method

A group of eight healthy, right-handed subjects (three male, five female) aged between 22 and 42 years participated (mean = 30.5 years). The stimuli consisted of 76 pictures from the Snodgrass and Vanderwart (1980) standardised set of line drawings. Half the items were pictures of living things and half were pictures of nonliving things. Within the living and nonliving categories, half the items had high name frequencies and half had low name frequencies. Pictures were pairwise matched on this basis (see Kucera & Francis, 1967, for name frequency norms). These items were taken from the BORB Test 14 and have been used in many studies of category-specificity (see e.g. Forde et al, 1997). Five living object categories (animals, birds, insects, fruit, and vegetables) and five nonliving categories (vehicles, furniture, tools, kitchen items, and clothing) were used. The pictures were presented as black-lined drawings on a grey-scaled background. Subjects were required to overtly name each picture as quickly and accurately as possible. On each trial 500msec of blank screen was followed by the central presentation of a white fixation point for 200msec. Subsequent to this, one of the 76 pictures was presented for 200msec. After the presentation of each picture the screen remained blank for 1500msec, upon which the next trial began (in total each subject saw 152 pictures presented in a random order; 76 presented twice).

5.5.2 Dipole source analysis

The aim of the dipole source analysis was to assess the temporal sequence involved in object recognition and naming and whether there were any observable differences between living and nonliving object categories. Dipole source analysis was performed separately for each subject in the following systematic fashion: The first peak of amplitude in the MEG waveform (post-stimulus) was found (e.g. typically around 80-100msec, see Figure 5.6), then a map showing the distribution of activation across all

MEG sensors at that latency was viewed in order to give a general idea of the region of interest (see Figure 5.7). Within this region a single dipole was positioned and fitted using DipoleFit (CTF Inc.). If the dipole regressed to the same position on five consecutive occasions the process continued to the next stage. This entailed widening the temporal window to include as much information as possible while remaining within three requirements set to determine how well the dipole modelled the time course of source activity: (1) Chi-squared goodness-of-fit error had to remain below eight, (2) Q-Moment value had to remain between 10 and 70 nanoampere-metres (nA-m), and (3) Monte-Carlo simulations, carried out to establish confidence volumes for each fitted dipole localisation, had to remain less than three cm3.

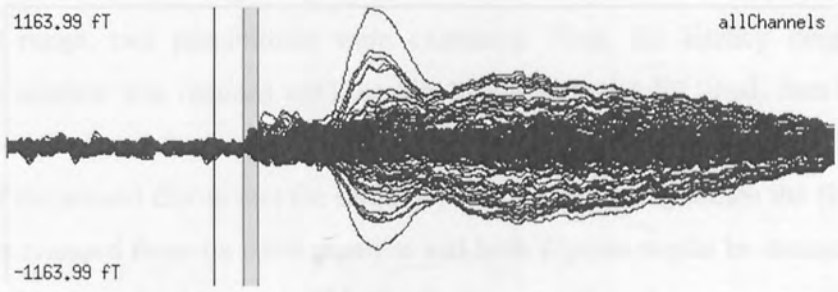


Figure 5.6. A MEG waveform showing activation across all 151 channels is shown. The black line represents the stimulus onset. The yellow sector represents the range (approximately 80-100msec) over which a dipole might be fitted.

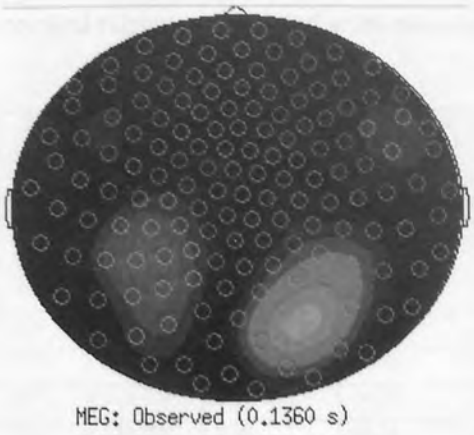


Figure 5.7. This illustrates a map of the distribution of activation across all MEG sensors used as a guide to finding a region of interest for dipole fitting.

If a successful fit over a single latency resulted in an unsuccessful fit over an extended temporal range, two possibilities were examined. First, the latency range of the temporal window was reduced until the dipole was successfully fitted, then the fitted dipole was fixed and the temporal window increased again before a second dipole was added. If the second dipole met the same requirements as the first then the first dipole would be released from its fixed position and both dipoles would be simultaneously fitted to the data. At this stage, if both dipoles moved to the same position in the model as was found when they were independently fitted, then, multi-dipole localisation was confirmed as successful. In contrast, if the fit was unreliable the second dipole would be removed and a single-dipole model accepted over the largest possible latency range given the aforementioned requirements. At this stage the process was repeated for the next determined peak.

5.5.3 Results

Out of eight subjects, only three produced one or more dipoles that met the requirements, and therefore, could be said to have successfully modelled the time-course of activity. The results are shown in Table 5.6 and discussed below.

Table 5.6. The cortical regions associated with successfully fitted dipoles for all eight subjects.

Subject	Dipole	Trigger	Peak (msec)	Range (msec)	Chi-squared error	Q-Moment	Monte-Carlo	Cortical Region
EF	1	Living	126	107-142	2.55	15.57	0.86	ROTPJ
EF	2	Living	232	200-243	5.36	28.25	1.02	RSFG
EF	1	Nonliving	181	157-192	4.95	40.34	2.23	RSTG
EF	2	Nonliving	224	200-240	4.81	26.56	1.59	RPCG
KS	1	Living	171	142-206	2.56	23.09	0.38	RPC
KS	2	Living	259	235-312	2.58	26.33	0.69	LLG
KS	1	Nonliving	171	136-206	3.70	42.13	0.77	RPC
KS	2	Nonliving	218	200-259	3.76	56.54	2.05	LLG
ES	1	Living	165	142-195	2.88	18.91	4.85	RPRCG

In Figure 5.8 the overall MEG waveform, and corresponding error and q-moment values are shown when subject KS named living things. Two dipoles were successfully modelled, the first accounted for a 64msec time window ranging from 142-206msec positioned in the right posterior cuneus (see Figure 5.8), the second accounted for a 77msec time window ranging from 235-312msec positioned in the left lingual gyrus (see Figure 5.9).

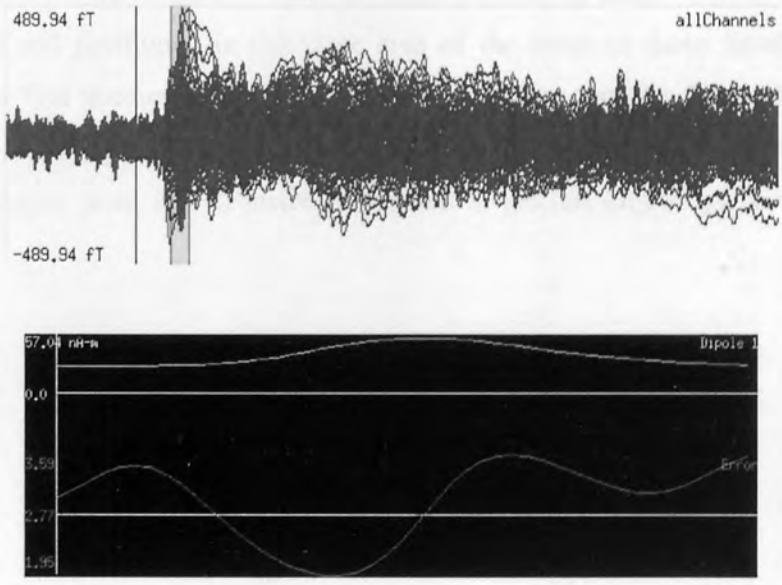


Figure 5.8. A single dipole fitted in the right posterior cuneus, over a range of 142-206msec, for subject KS when he named living things.

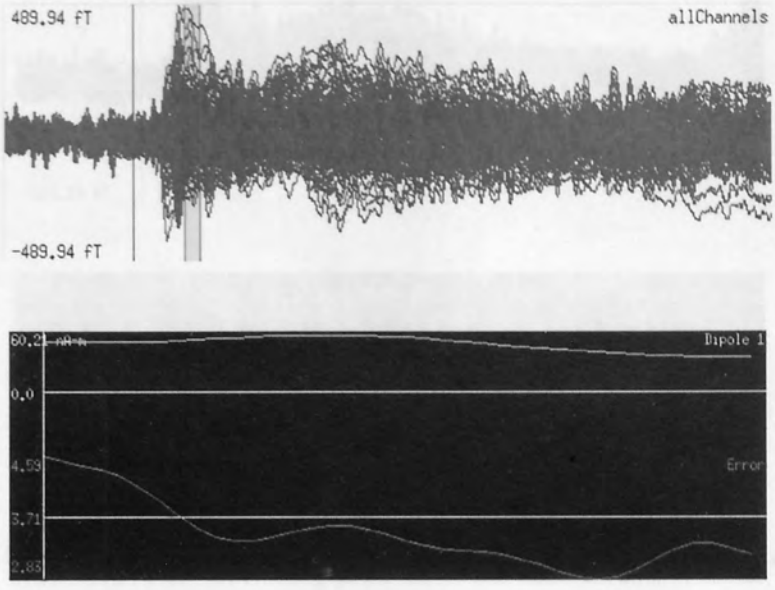


Figure 5.9. A single dipole fitted in the left lingual gyrus, over a range of 235-312msec, for subject KS when he named living things.

In Figure 5.10 the overall MEG waveform, and corresponding error and q-moment values are shown for subject KS when he named nonliving things. Again, two dipoles were fitted and positioned in the same area of the brain as those fitted for living things. The first accounted for a 70msec time window ranging from 136-206msec positioned in the right posterior cuneus (see Figure 5.10), the second a 59msec time window ranging from 200-259msec positioned in the left lingual gyrus (see Figure 5.11).

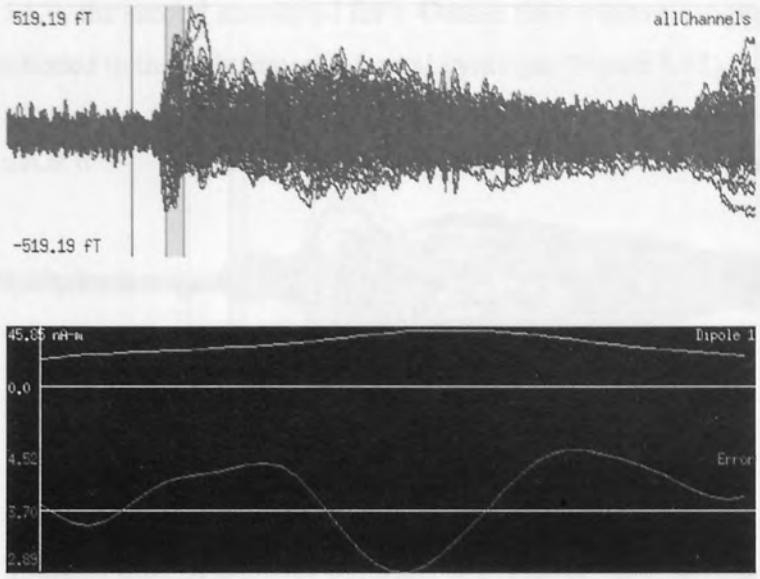


Figure 5.10. A single dipole fitted in the right posterior cuneus, over a range of 136-206msec, for subject KS when he named nonliving things.

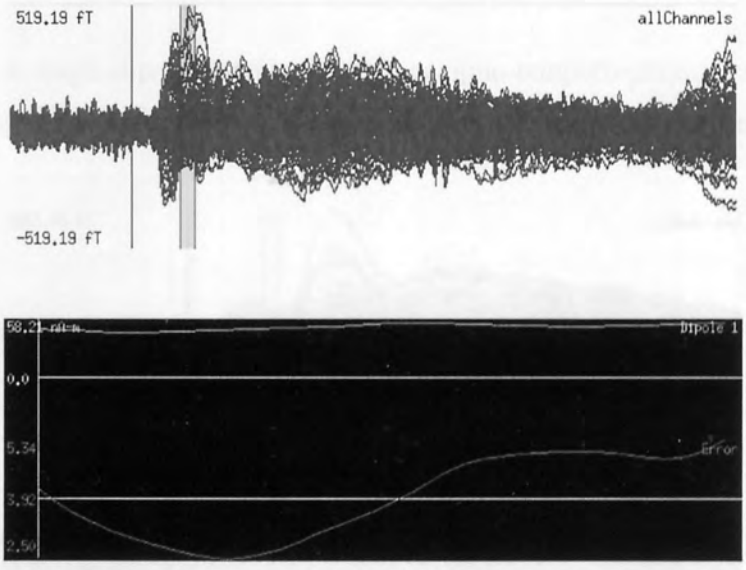


Figure 5.11. A single dipole fitted in the left lingual gyrus, over a range of 200-259msec, for subject KS when he named nonliving things.

In Figure 5.12 the overall MEG waveform, and corresponding error and q-moment values are shown when subject EF named living things. Two dipoles were successfully modelled to the data, the first accounted for a 35msec time window ranging from 107-142msec positioned in the right occipital-temporo-parietal junction

(see Figure 5.12), the second accounted for a 43msec time window ranging from 200-243msec positioned in the right superior frontal gyrus (see Figure 5.13).

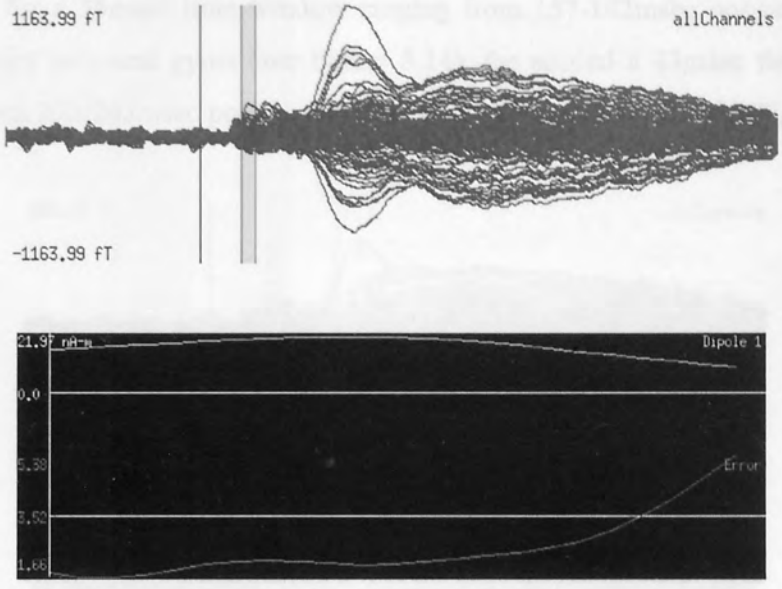


Figure 5.12. A single dipole fitted in the right occipito-temporo-parietal junction, over a range of 107-142msec, for subject EF when she named living things.

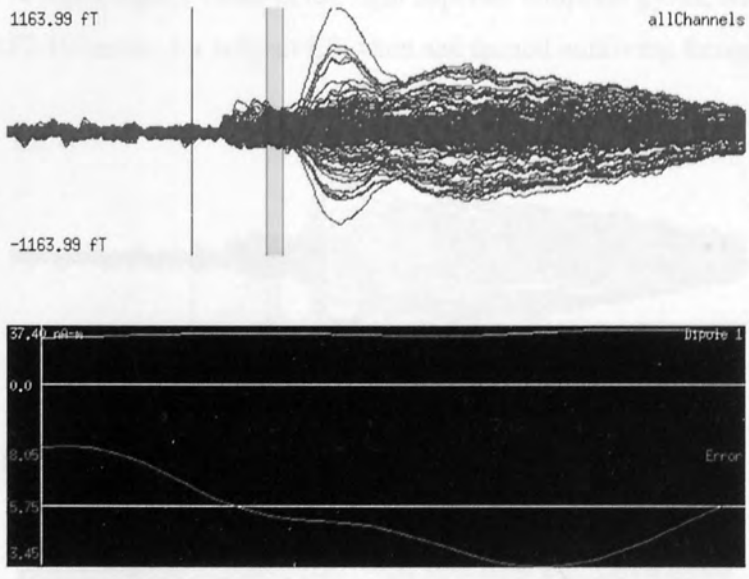


Figure 5.13. A single dipole fitted in the right superior frontal gyrus, over a range of 200-243msec, for subject EF when she named living things.

In Figure 5.14 the overall MEG waveform, and corresponding error and q-moment values are shown when EF named nonliving things. Again, two dipoles were fitted and positioned in the same area of the brain as those fitted for living things. The first accounted for a 35msec time window ranging from 157-192msec positioned in the right superior temporal gyrus (see Figure 5.14), the second a 43msec time window ranging from 200-243msec positioned in the right postcentral gyrus (see Figure 5.15).

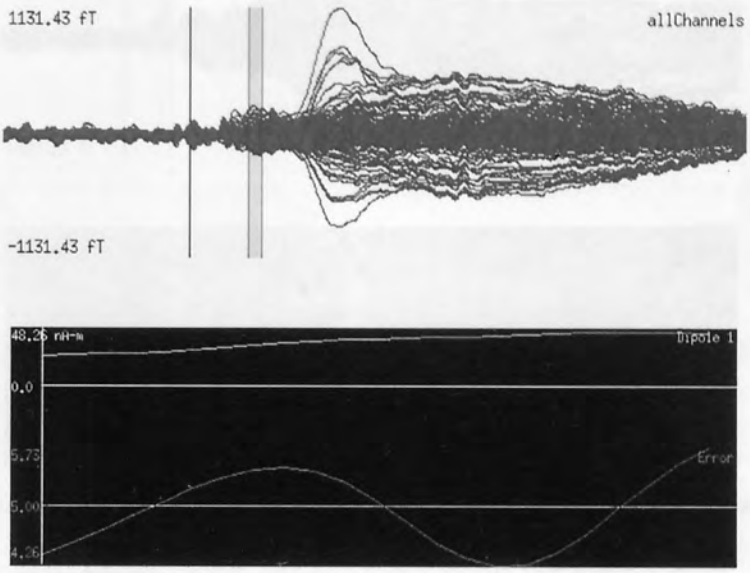


Figure 5.14. A single dipole fitted in the right superior temporal gyrus, over a range of 157-192msec, for subject EF when she named nonliving things.

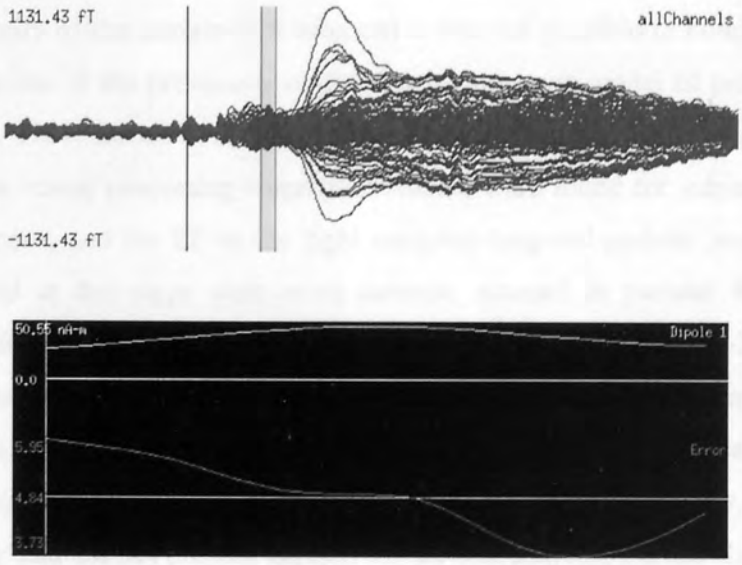


Figure 5.15. A single dipole fitted in the right postcentral gyrus, over a range of 200-243msec, for subject EF when she named nonliving things.

The final dipole fitted was for subject ES. In Figure 5.16 the overall MEG waveform, and corresponding error and q-moment values are shown when ES named living things. The dipole accounted for a 53msec time window ranging from 142-195msec positioned in the right precentral gyrus (see Figure 5.16).

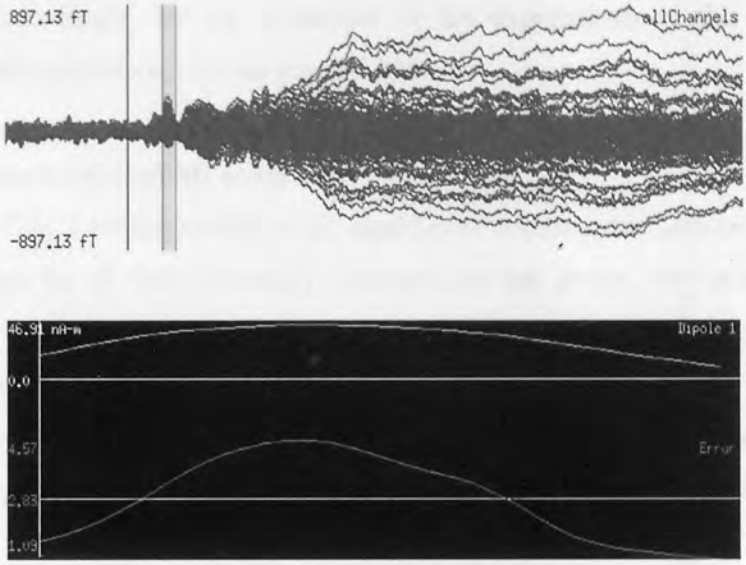


Figure 5.16. A single dipole fitted in the right precentral gyrus, over a range of 142-195msec, for subject ES when she named living things.

5.5.4 Discussion

The main finding from the dipole fitting was the lack of consistency across subjects: For the majority of the sample (5/8 subjects) it was not possible to obtain any stable dipoles. In terms of the previously outlined temporal stage model of picture naming (Levelt et al, 1991; Levelt et al, 1998) there were few similarities: Occipital sources located at the visual processing stage (0-150msec) were found for subject KS in the posterior cuneus, and for EF in the right occipital-temporal-parietal junction. Other sources found at this stage were more anterior, situated in parietal and temporal cortices. Right parietal sources were found during lemma selection (150-275msec) for EF in the postcentral gyrus, and for ES in the precentral gyrus, however, for KS the lingual gyrus was also located during this stage. In terms of the cortical areas most often implicated in functional imaging studies of category-specificity, the present dipole fitting data did not provide support for the role played by either the left middle temporal gyrus (in identifying nonliving relative to living things), or the left inferior frontal gyrus (for living relative to nonliving things).

This difficulty in modelling source activity by dipole fitting was perhaps not altogether surprising. As was previously mentioned, dipole source analysis has been successfully employed in conventional evoked-potential experiments, but cognitive tasks such as those carried out in this chapter are inherently difficult to model because the data is non-phase-locked to the stimulus and large discrete areas of cortex may be involved. Accordingly, for the remainder of the experiments in this chapter the analytical technique of choice was group-SAM.

5.5.4.1 Group-SAM (SnPM) analysis

In Tables 5.7 to 5.10 the results of all significant comparisons between active and baseline states for all time-frequency combinations are shown. For baseline (half a second prior to picture presentation) compared to active states there was an extensive amount of activity detected throughout. In the six frequency bands analysed no significant power increases were found when the active state was compared to the passive state, only power decreases, i.e., there was no significant ERS, only ERD.

Living (0-300msec) compared to baseline

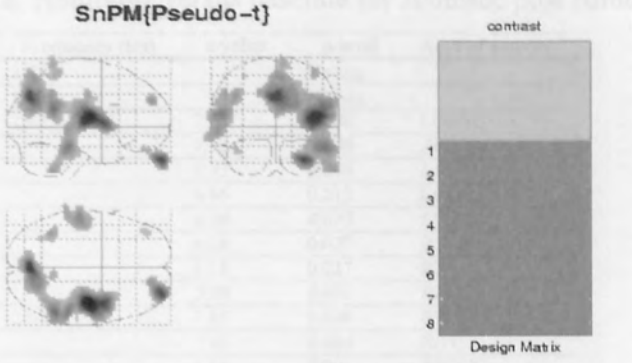
Table 5.7 shows the size and anatomical position of the significant effects for all baseline state (500msec, pre-stimulus) relative to active state (0-300msecs) for living things at all frequency bands.

Table 5.7. Living versus baseline for 300msec post stimulus

Frequency (Hz)	t-value	p-level	Area of activity
5-15	5.95	0.023	LSLXN
10-20	6.86	0.016	RMTG
	6.05	0.031	LCBAL
	5.74	0.047	RTSBG
15-25	10.33	0.004	RSLI
	9.09	*0.004*	*IC*
	7.74	*0.004*	*RTSMG*
	7.21	0.004	LPCG
	6.46	*0.016*	*LMTG*
	6.32	*0.020*	*LPCG*
	6.70	0.008	RSFG
	6.56	0.012	LIPG
	5.59	*0.043*	*LPPC*
	6.16	0.031	RPCG
	5.78	0.035	LSPG
20-30	7.00	0.016	RTSBG
	6.09	0.023	RPC
25-35	7.13	0.008	LSTG'
	7.00	0.008	RSFG
	6.85	0.008	LMTG
	6.21	*0.023*	*LSTG*
	6.46	0.012	LPCG
	6.39	0.016	LMFG
	6.14	0.031	RSFG
	6.00	0.039	RPCG
	5.85	0.047	RPHG
30-40		Not sig	

Note that areas in italics are significant voxels proximal to the previous non-italicised voxel within the same cluster.

Figure 5.17 represents the significant voxels found in the 15-25Hz frequency range using the SnPM voxel-level inference method. A large area of desynchronisation was found extending on the right of anterior and inferior parietal regions, and on the left of anterior parietal and middle temporal regions. An area of the right superior frontal gyrus was also significantly active.



P values & statistics: ./nam0.3Lvbaseline15-25Hz

region	size (k)	PseudoP(T_m >= u)		(x,y,z) mm
1	3535	10.33	0.004	42 -15 12
		9.09	0.004	0 -75 36
		7.74	0.004	51 -51 24
2	245	8.50	0.004	30 63 -36
3	515	7.21	0.004	-60 -24 15
		6.46	0.016	-63 -36 -3
		6.32	0.020	-54 -15 39
4	67	6.70	0.008	18 54 33
5	101	6.56	0.012	-42 -51 39
		5.59	0.043	-33 -66 42
6	47	6.17	0.031	9 -51 75
7	40	6.16	0.031	42 -48 63
8	10	5.78	0.035	-33 -54 60
9	4	5.74	0.035	-66 12 27
10	22	5.61	0.043	-39 48 -27
11	1	5.53	0.043	45 54 30

alpha = 0.0500, df = 7 Critical threshold = 5.3982
Volume = 141139 3.00x 3.00x 3.00 mm voxels
Design: Multisubject, 1 scan per subj; 8(subj)
Perms: 256 permutations of conditions, bhPerms=1
Pseudo-t: Variance smoothed with FWHM [12x12x12] mm

Figure 5.17. This figure illustrates the significant results found by the SnPM analysis for baseline state (500msec, pre-stimulus) relative to active state (0-300msecs) for living things in the 15-25Hz frequency band.

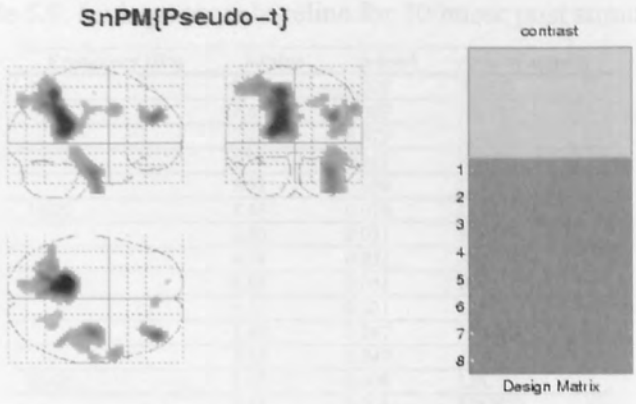
Nonliving (0-300msec) compared to baseline

Table 5.8 shows the size and anatomical position of the significant effects for all baseline states (500msec, prestimulus) relative to active states (0-300msecs) for nonliving things at all frequency bands.

Table 5.8. Nonliving versus baseline for 300msec post stimulus

Frequency (Hz)	t-value	p-level	Area of activity
5-15		Not sig	
10-20		Not sig	
15-25	7.98	0.008	LOSBG
	7.92	*0.008*	*RC*
	7.92	*0.008*	*LPC*
	6.86	0.012	LPCG
	6.38	*0.027*	*LSTG*
	6.28	0.027	RSTG
	6.11	0.027	RI
	5.99	*0.031*	*RPCG*
20-30	7.85	0.004	RPHG
	7.41	*0.004*	*RITG*
	6.86	0.004	RPOCG
	6.22	0.016	LOC
	5.91	0.020	RSFG
25-35	9.71	0.004	LSBXN
	8.69	*0.004*	*LPC*
	6.99	*0.020*	*LSPG*
	7.54	0.008	RU
	7.20	*0.012*	*RITG*
	6.72	0.020	RMFG
	6.49	*0.020*	*RSTG*
	6.27	*0.020*	*RIPG*
	6.11	0.027	RMFG
	6.03	0.035	RSPG
	5.73	*0.047*	*RPC*
	5.58	*0.047*	*RPC*
	5.74	0.047	LCPD
30-40		Not sig	

Figure 5.18 shows the SnPM voxel-level results at the 25-35Hz frequency band. A large area of desynchronisation was found extending on the left superior parietal lobe, extensively throughout the right temporal lobe, and ranging over right anterior parietal through to right medial frontal regions. An area of activation was also found in the left cerebellum.



P values & statistics: /nam0.3NLvbaseline25-35Hz

region	size (k)	PseudoP(T$_{max}$ >= u)		(x,y,z) mm
1	2006	9.71	0.004	-15 -42 21
		8.69	0.004	-12 -54 54
		6.99	0.020	-33 -57 60
2	208	7.78	0.004	39 48 30
3	643	7.54	0.008	36 -15 -30
		7.20	0.012	39 -12 -39
		7.11	0.016	36 -12 -48
4	348	6.72	0.020	60 6 39
		6.49	0.020	42 -45 15
		6.27	0.020	48 -27 24
5	21	6.11	0.027	6 45 27
6	73	6.03	0.035	30 -54 48
		5.73	0.047	21 -51 45
		5.58	0.047	21 -66 42
7	3	5.74	0.047	-33 -75 -21
8	3	5.58	0.047	-15 57 36
9	1	5.57	0.047	63 -15 54

alpha = 0.0500, df = 7 Critical threshold = 5.4925
Volume = 141546 3.00x 3.00x 3.00 mm voxels
Design: Multisubject, 1 scan per subj: 8(subj)
Perms: 256 permutations of conditions, bhPerms=1
Pseudo-t: Variance smoothed with FWHM [12x12x12] mm

Figure 5.18. This figure illustrates the significant results found by the SnPM analysis for baseline state (500msec, pre-stimulus) relative to active state (0-300msecs) for nonliving things in the 25-35Hz frequency band.

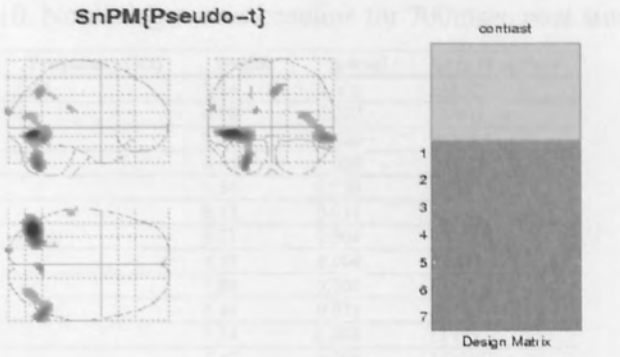
Living (0-700msec) compared to baseline

Table 5.9 shows the size and anatomical position of the significant effects for all baseline states (500msec, prestimulus) relative to active states (0-700msecs) for living things at all frequency bands.

Table 5.9. Living versus baseline for 700msec post stimulus

Frequency (Hz)	t-value	p-level	Area of activity
5-15	8.54	0.008	RMFG
	7.60	*0.008*	*RMFG*
	7.10	*0.012*	*LMFG*
	6.76	0.012	RMOG
	5.51	0.039	LOC
10-20	8.43	0.016	LIOG
	6.50	0.031	RMTG
	6.34	*0.031*	*RMOG*
	6.65	0.031	RPC
	6.21	0.031	LIPG
	5.89	0.047	LPSBG
	5.88	*0.047*	*LSPG*
15-25	8.05	0.008	LPC
	7.65	0.008	LPOCG
	6.67	0.020	LMOG
	6.23	*0.023*	*LCPD*
	6.48	0.020	RSPG
20-30	6.00	0.020	LPSMG
	5.96	0.020	ROPC
	5.71	0.023	LIPG
	5.64	0.023	RTSBG
	5.54	*0.027*	*RTSBG*
25-35		Not sig	
30-40		Not sig	

Figure 5.19 shows the SnPM voxel-level results at the 10-20Hz frequency band. A large area of desynchronisation was found extending on the left side of the inferior occipital gyrus, medial temporal lobe and inferior parietal region. Right hand side activation was concentrated in more medial occipital and temporal regions, as well as more anterior parietal areas.



P values & statistics: ./nam0.7Lvbaseline10-20Hz

region	size (k)	Pseudo-t		(x,y,z) mm
1	570	8.43	0.016	-42 -72 -6
		7.26	0.023	-27 -69 -42
2	292	7.08	0.023	60 -63 -12
		6.50	0.031	51 -60 0
		6.34	0.031	36 -78 15
3	51	6.65	0.031	6 -66 45
4	14	6.52	0.031	-15 -102 21
5	19	6.21	0.031	-63 -33 24
6	12	5.89	0.047	-21 -51 39
		5.88	0.047	-21 -60 45

alpha = 0.0500, df = 6 Critical threshold = 5.7187
Volume = 141550 3.00x 3.00x 3.00 mm voxels
Design: Multisubject, 1 scan per subj: 7(subj)
Perms: 128 permutations of conditions, blkPerms=1
Pseudo-t: Variance smoothed with FWHM [12x12x12] mm

Figure 5.19. This figure illustrates the significant results found by the SnPM analysis for baseline state (500msec, pre-stimulus) relative to active state (0-700msecs) for living things in the 10-20Hz frequency band.

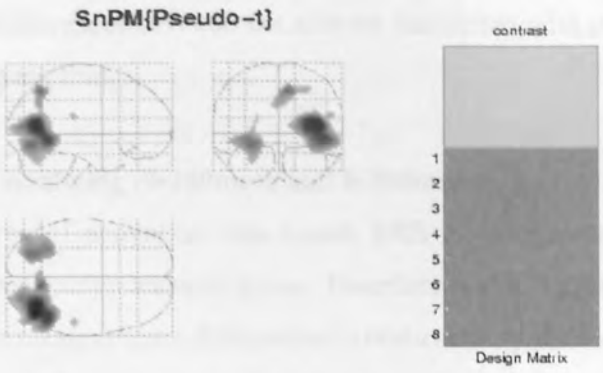
Nonliving (0-700msec) compared to baseline

Table 5.10 shows the size and anatomical position of the significant effects for all baseline states (500msec, prestimulus) relative to active states (0-700msecs) for nonliving things at all frequency bands.

Table 5.10. Nonliving versus baseline for 700msec post stimulus

Frequency (Hz)	t-value	p-level	Area of activity
5-15	7.04	0.016	LMFG
	6.20	*0.027*	*LMFG*
	6.88	0.020	ROC
	6.75	*0.020*	*RMTG*
	6.34	0.020	LTSB
	6.13	0.031	LLG
10-20	9.71	0.004	RTSBG
	8.51	*0.004*	*RMOG*
	7.88	0.008	RPC
	6.44	*0.023*	*RSPG*
	7.74	0.008	LFFG
	7.47	*0.008*	*LOSBG*
	5.92	*0.047*	*LTSG*
	6.27	0.023	RIPG
15-25	7.34	0.012	LCPD
	6.96	0.020	LPOCG
	6.08	0.039	RSPG
	6.03	0.039	RMTG
	6.02	0.039	ROMTG
20-30	8.17	0.004	ROC
	5.41	*0.043*	*RPC*
	5.44	0.043	LIPG
	5.33	0.047	RFFG
	5.31	0.047	RSPG
25-35		Not sig	
30-40		Not sig	

Figure 5.20 shows the SnPM voxel-level results at 10-20Hz. A large area of desynchronisation was found extending on the left side of the inferior occipital gyrus, medial temporal lobe and inferior parietal region. Right hand side activation was concentrated in more medial occipital and temporal regions, as well as more anterior parietal areas.



P values & statistics: ./nam0.7NLvbaseline10-20Hz

region	size (k)	Pseudo-t	P(T_max >= u)	(x,y,z) mm
1	1513	9.71	0.004	39 -69 12
		8.51	0.004	48 -57 -6
2	208	7.88	0.008	12 -63 51
		6.44	0.023	27 -60 51
3	693	7.74	0.008	-27 -75 -12
		7.47	0.008	-33 -57 -6
		5.92	0.047	-24 -54 15
4	14	6.27	0.023	54 -30 21

alpha = 0.0500, df = 7 Critical threshold = 5.8011
Volume = 141546 3.00x 3.00x 3.00 mm voxels
Design: Multisubject, 1 scan per subj: 8(subj)
Perms: 256 permutations of conditions, bhPerms=1
Pseudo-t: Variance smoothed with FWHM [12x12x12] mm

Figure 5.20. This figure illustrates the significant results found by the SnPM analysis for baseline state (500msec, pre-stimulus) relative to active state (0-700msecs) for nonliving things in the 10-20Hz frequency band.

In summary, the results for both 0-300msec and 0-700msec comparisons with the baseline state showed that group-SAM analysis elucidated a number of areas of cortical activity associated with the naming of objects. In terms of the frequency bands, there was consistent alpha activity (in the 5-15Hz range) over frontal areas, and large amounts of beta activity (in 10-20Hz and 15-25Hz ranges) over a number of parietal and occipital areas (and to a lesser extent temporal regions as well). However, the comparison was between living things and fixation (baseline condition) and between nonliving things and fixation, and consequently it was not surprising that a large number of areas were activated. The main aim of the current work was, however, to examine differences in the visual processing of living and nonliving things and consequently, in the following section and in all subsequent experiments,

the focus was on differences between the activity associated with *direct* comparisons of living and nonliving things.

Living relative to nonliving (0-300msec and 0-700msec)

One significant area of activation was found: ERS at 0-700msec, 15-25Hz, for a cluster in the right parahippocampal gyrus. Therefore, when subjects named objects out loud there were no significant differences in brain activity for eleven out or twelve possible time-frequency comparisons between naming living and nonliving things. Figure 5.21 illustrates the difference that was found using the cluster inference method in SnPM.

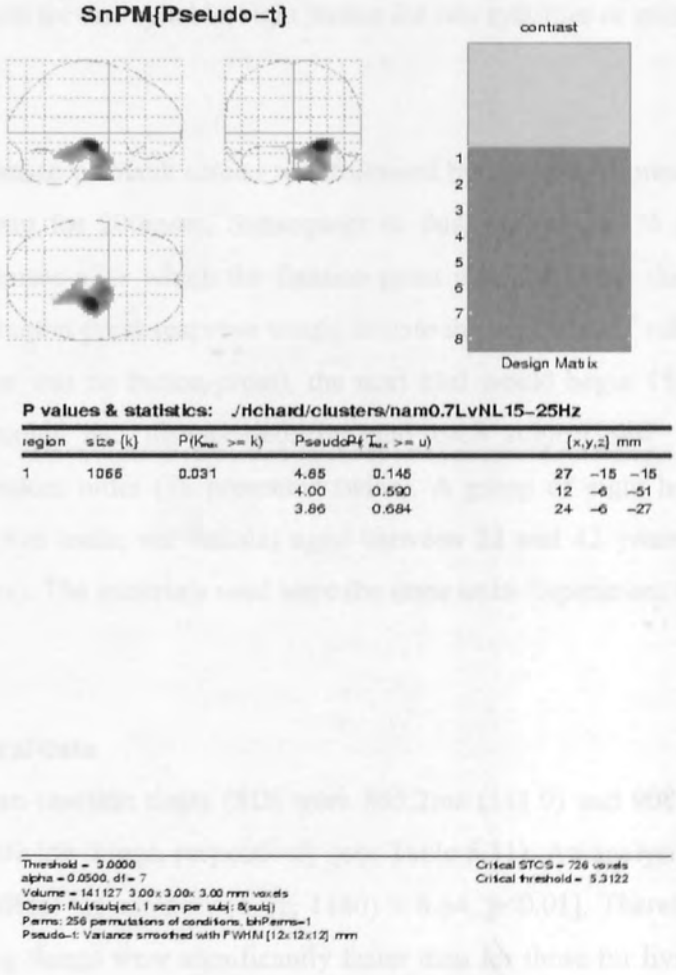


Figure 5.21. For the direct comparison of living and nonliving things, SnPM found one significant area of ERS over 0-700msec, in the 15-25Hz frequency band, for a cluster in the right parahippocampal gyrus.

5.6 Experiment 2: Naming (covertly) living and nonliving things

Facial and jaw movement by subjects can cause problems when recording MEG experiments, and although instructions were given to subjects to name items with as little movement as possible an overt naming paradigm remains open to such artefacts. For example, in Figure 5.14 a dipole was initially fitted to the large amplitude at around 400-600msec, however, when the voxel was superimposed onto the subject's MRI it was found to be outside the head, in the jaw area. In addition, in the overt naming paradigm no behavioural data (e.g. reaction times and accuracy) was obtained to ensure subjects were performing the task correctly. Consequently, a different paradigm was used for naming in Experiment 2, whereby subjects were required to respond by button-press depending on the number of syllables in the name of each stimulus (left button for one syllable, right button for two syllables or more).

5.6.1 Method

On each trial 500msec of blank screen was followed by the central presentation of a white fixation point for 200msec. Subsequent to this, one of the 76 pictures was presented for 200msec after which the fixation point returned. After the picture had been presented a button-press response would initiate the next trial. If subjects did not respond (i.e., there was no button-press), the next trial would begin 1500msec after the previous stimulus had disappeared. In total each subject saw 152 pictures presented in a random order (76 presented twice). A group of eight healthy, right-handed subjects (two male, six female) aged between 22 and 42 years participated (mean = 33.8 years). The materials used were the same as in Experiment 1.

5.6.2 Results

5.6.2.1 Behavioural data

The subjects' mean reaction times (SD) were 865.2ms (311.0) and 908.7ms (311.8) for living and nonliving things, respectively (see Table 5.11). An analysis of variance revealed a main effect for category [$F(1, 1140) = 6.64$, $p<0.01$]. Therefore, reaction times for nonliving things were significantly faster than for those for living things. A similar number of errors were found for living (1.4%) and nonliving (1.6%) things.

Table 5.11. Behavioural data from experiments 2 to 5.

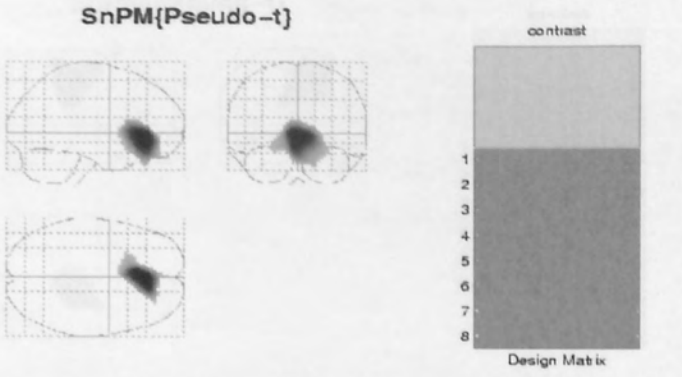
Experiment	Condition	RT (msec)	*SD*	Errors (%)
2. Naming covertly	Living	865.2	311.0	1.4
	Nonliving	908.7	311.8	1.6
3. Categorising	Living	645.6	268.9	0.0
	Nonliving	687.1	276.1	0.7
4. Visual configuration (naming)	ML	330.5	152.9	2.2
	MNL	339.2	150.0	1.1
	SL	358.8	172.1	2.2
	SNL	347.1	161.8	0.6
5. Visual configuration (categorising)	ML	336.8	146.0	3.3
	MNL	343.5	154.7	0.6
	SL	320.8	129.2	0.6
	SNL	352.7	160.0	0.6

5.6.2.2 Group-SAM (SnPM) analysis

In Appendix C the results of all significant comparisons between active and baseline states for all time-frequency combinations are shown. In accord with the findings from the first experiment, for baseline (half a second prior to picture presentation) compared to active states there was extensive activity throughout. In the six frequency bands analysed no significant power increases were found when the active state was compared to the baseline state, only power decreases, i.e., there was no significant ERS, only ERD.

Living relative to nonliving (0-300msec and 0-700msec)

Two significant areas of activation were found for the living versus nonliving comparison: (1) ERD at 300msec, 20-30Hz, a cluster of bilateral activation in the anterior cingulate region of the limbic lobe, and (2) ERD at 300msec, 25-35Hz, in the right frontal lobe, a cluster extending over the post and precentral gyrus. Therefore, when subjects named objects covertly there were significant differences in cortical activity for two out of twelve possible time-frequency comparisons between naming living and nonliving things. Figures 5.22 and 5.23 illustrate the differences that were found using the cluster level analysis of SnPM.



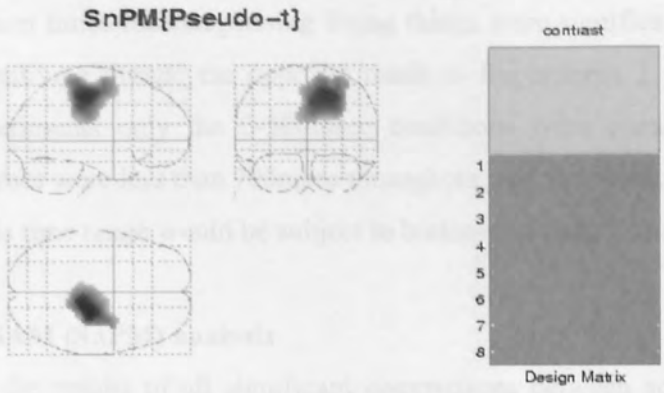
P values & statistics: ./richard/clusters/syl0.3LvNL20-30Hz

region	size {k}	P(K_{max} >= k)	Pseudo-P(T_{max} >= u)		{x,y,z} mm
1	1345	0.031	5.31	0.156	0 33 -6
			3.07	1.000	0 57 -27

Threshold = 3.0000
alpha = 0.0500, df = 7
Volume = 142728 3.00 x 3.00 x 3.00 mm voxels
Design: Multisubject, 1 scan per subj: 8(subj)
Perms: 64 permutations of conditions, bhPerms=0
Pseudo-t: Variance smoothed with FWHM [12 x 12 x 12] mm

Critical STCS = 1030 voxels
Critical threshold = 5.9242

Figure 5.22. This figure illustrates the significant SnPM result showing ERD at 300msec, 20-30Hz for a cluster of bilateral activation in the anterior cingulate region of the limbic lobe.



P values & statistics: ./richard/clusters/syl0.3LvNL25-35Hz

region	size (k)	$P(K_{max} >= k)$	Pseudo$P(T_{max} >= u)$		(x,y,z) mm
1	1648	0.020	5.32	0.094	21 -24 48

Threshold = 3.0000
alpha = 0.0500, df = 7
Volume = 141846 3.00x3.00x3.00 mm voxels
Design: Multisubject, 1 scan per subj: 8(subj)
Perms: 256 permutations of conditions, bhPerms=1
Pseudo-t: Variance smoothed with FWHM [12x12x12] mm

Critical STCS = 928 voxels
Critical threshold = 5.5467

Figure 5.23. This figure illustrates the significant SnPM result showing ERD at 300msec, 25-35Hz, for a cluster extending over the post and precentral gyri.

5.7 Experiment 3: Categorising living and nonliving things

5.7.1 Method

A group of eight healthy, right-handed subjects (two male, six female) aged between 22 and 46 years participated (mean = 29.6 years). The materials used were the same as Experiment 1. The procedure and was the same as Experiment 2 except subjects were required to categorise each picture as either a living or nonliving thing.

5.7.2 Results

5.7.2.1 Behavioural data

The subjects' mean reaction times (SD) and errors are shown in Table 5.11. An analysis of variance revealed a main effect for category [F (1, 1140) = 6.64, $p<0.01$].

Therefore, reaction times for categorising living things were significantly faster than for those for nonliving things; the opposite result to Experiment 2. In this and all subsequent experiments only the 0-300msec conditions were considered because mean reaction times were less than 700msec throughout, and therefore, any significant findings over this time range would be subject to button-press artefacts.

5.7.2.2 Group-SAM (SnPM) analysis

In Appendix C the results of all significant comparisons between active states and baseline for all time-frequency combinations are shown. For baseline (half a second prior to picture presentation) compared to active states there was extensive significant activity throughout. Once again, in the six frequency bands analysed no significant power increases (ERS) were found when the active state was compared to the passive state, only power decreases (ERD).

Living relative to nonliving (0-300msec)

A single significant area of activation was found: (1) ERD at 300msec, 10-20Hz, individual voxel activation in the right superior frontal gyrus. Therefore, when subjects categorised objects there was a significant difference in cortical activity for one out or six possible time-frequency comparisons between categorising living and nonliving things. Figure 5.24 illustrates the difference that was found using the voxel level analysis of SnPM.

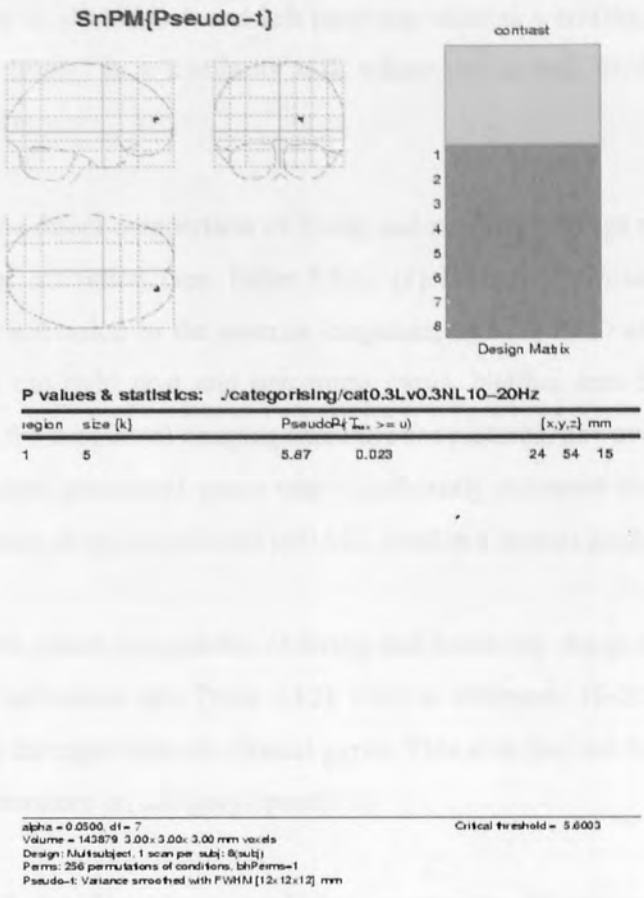


Figure 5.24. This figure illustrates the significant SnPM result showing ERD at 300msec, 10-20Hz, for a voxel in the right superior frontal gyrus.

5.7.3 Summary of results for experiments 1-3

In Experiment 1, two methods of analysis were employed to investigate the neural correlates of the naming of living and nonliving things. Dipole modelling was relatively ineffective with only three out of eight subjects having any dipoles successfully modelled. This data was included as a demonstration that dipole fitting may not be a particularly suitable analytical technique for MEG studies on complex cognitive tasks, such as picture naming. In contrast, group-SAM analysis provided reliable results across subjects. Indeed, SAM only identifies areas that are statistically significant across the group of subjects. The direct comparison of living and nonliving things resulted in only one significant difference out of twelve possible comparisons: ERS at 700msec, 15-25Hz, for a cluster in the right parahippocampal gyrus (see Table 5.12). This result has no corresponding finding in the functional imaging literature,

although Mummery et al (1998) found left parahippocampal activation for nonliving things (relative to living) in a similarity task where the stimuli used were written words (see Table 5.1).

In Experiment 2, the direct comparison of living and nonliving things resulted in two significant areas of activation (see Table 5.12): (1) ERD at 300msec, 20-30Hz, a cluster of bilateral activation in the anterior cingulate, and (2) ERD at 300msec, 25-35Hz, a cluster in the right post and precentral gyrus. Neither area had previously been implicated in the functional imaging literature for pictures, however, Devlin et al (2002) found the right precentral gyrus was significantly activated for living things compared to nonliving at an uncorrected $p<0.001$ level in a lexical decision task.

In Experiment 3, the direct comparison of living and nonliving things resulted in one significant area of activation (see Table 5.12): ERD at 300msec, 10-20Hz, individual voxel activation in the right superior frontal gyrus. This area had not been previously implicated in the literature on category-specificity

Table 5.12. All significant living-nonliving comparisons in experiments 1-3.

Experiment	Condition	Timing (sec)	Frequency (Hz)	Area(s) of activity
1. Naming overtly	L v NL	0.7 v 0.7	15-25	RPHG
2. Naming covertly	L v NL	0.3 v 0.3	20-30	BAC
2. Naming covertly	L v NL	0.3 v 0.3	25-35	RFPOCG and RFPCG
3. Categorising	L v NL	0.3 v 0.3	10-20	RSFG

5.8 Experiment 4: Naming (covertly)

5.8.1 Method

A group of eight healthy, right-handed subjects (three male, five female) aged between 24 and 46 years participated (mean = 30.3 years). The stimuli consisted of 60 pictures from the [3]Moore and Price (1999) study These stimuli were equally divided into four groups: 1) multicomponent living things (ML) (animals), 2) multicomponent nonliving things (MNL) (e.g. vehicles), 3) simple shaped living things (SL) (fruit and vegetables), 4) simple shaped nonliving things (SNL) (e.g. tools). Pictures were pairwise matched across conditions for word frequency (see Kucera & Francis, 1967,

[3] I would like to thank Caroline Moore and Cathy Price for kindly permitting the use of their pictures in my experiments.

for name frequency norms). The pictures were presented as black-lined drawings on a grey-scaled background. The procedure was the same as in Experiment 2 except that in total each subject saw 120 pictures, presented in a random order (60 presented twice).

5.8.2 Results

5.8.2.1 Behavioural data

The subjects' mean reaction times (SD) and errors are shown in Table 5.11. An analysis of variance revealed no effect of condition-type [F (1, 672) = 0.96, NS]. Post hoc multiple comparisons showed no significant differences between any of the four conditions (Tukey HSD, NS). This indicated that the four conditions were of comparable difficulty, and therefore, the interpretation of any differences in activity was unlikely to be confounded by overall task difficulty.

5.8.2.2 Group-SAM (SnPM) analysis

The following comparisons were made across all frequency bands for 0-300msec: 1) ML versus MNL, 2) ML versus SL, 3) SL versus SNL, and 4) SNL versus MNL.

ML relative to MNL (0-300msec)

No significant areas of activation were found in any of the six frequency bands.

ML relative to SL (0-300msec)

A single significant area of activation was found: ERS at 0-300msec, 15-25Hz, individual voxel activation in the right posterior cerebellar tonsil. Therefore, when subjects named living things with different visual configurations there was a significant difference in cortical activity for one out or six possible frequency bands. Figure 5.25 illustrates the difference that was found using the voxel level analysis of SnPM.

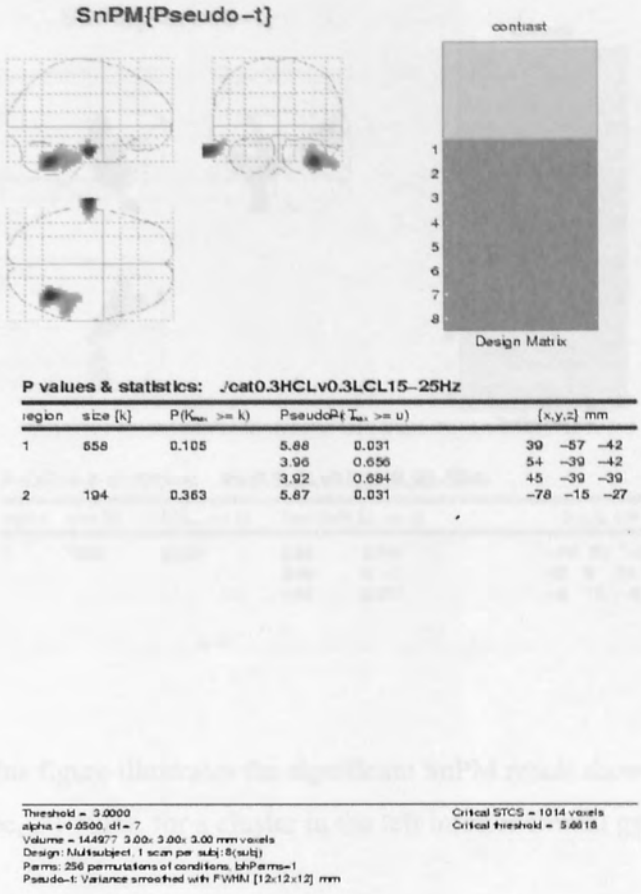
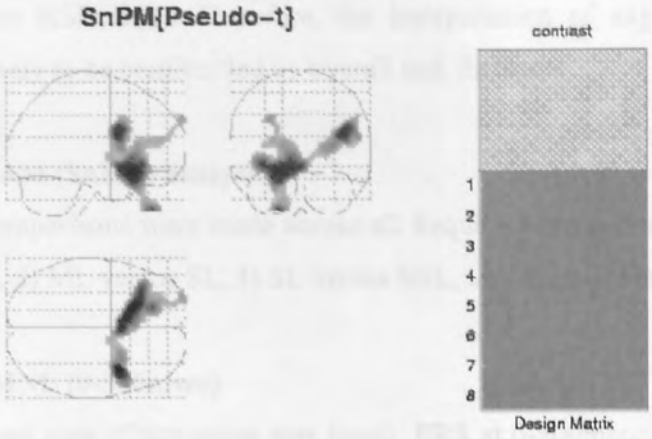


Figure 5.25. This figure illustrates the significant SnPM result showing ERS at 300msec, 15-25Hz, for a cluster in the right posterior cerebellar tonsil.

SL relative to SNL (0-300msec)

A single significant area of activation was found: ERS at 0-300msec, 20-30Hz, for a cluster in the left inferior frontal gyrus. Therefore, when subjects named simple shaped living and nonliving things there was a significant difference for one out of six frequency bands. Figure 5.26 illustrates the difference that was found using the cluster level analysis of SnPM.



P values & statistics: ./cat0.3LCLv0.3LCNL20-30Hz

region	size (k)	P(K_{max} >= k)	PseudoP(T_{max} >= u)		{x,y,z} mm
1	1578	0.035	5.53	0.074	-18 21 -15
			5.26	0.141	42 9 24
			4.90	0.227	-3 12 -9

Figure 5.26. This figure illustrates the significant SnPM result showing ERS at 300msec, 20-30Hz, for a cluster in the left inferior frontal gyrus.

SNL relative to MNL (0-300msec)

No significant regions of activity were found in any of the six frequency bands.

5.9 Experiment 5: Categorising

5.9.1 Method

A group of eight healthy, right-handed subjects (four male, four female) aged between 24 and 46 years participated (mean = 30.3 years). The materials used were the same as Experiment 4. The procedure was the same as Experiment 4 except subjects were required to categorise each picture as either a living or nonliving thing.

5.9.2 Results

5.9.2.1 Behavioural data

The subjects' mean reaction times (SD) and errors are shown in Table 5.11. An analysis of variance revealed no effect of condition [F (1, 679) = 1.42, NS]. Post hoc multiple comparisons showed no significant differences between any of the four

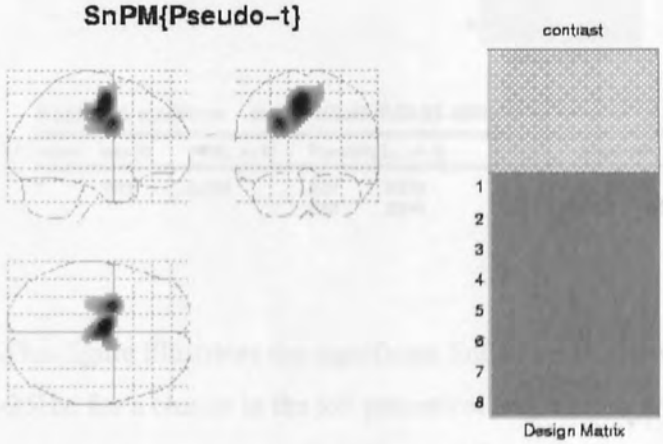
conditions (Tukey HSD, NS). Therefore, the interpretation of any differences in activity was unlikely to be confounded by overall task difficulty.

5.9.2.2 Group-SAM (SnPM) analysis

The following comparisons were made across all frequency bands for 0-300msec: 1) ML versus MNL, 2) ML versus SL, 3) SL versus SNL, and 4) SNL versus MNL.

ML relative to MNL (0-300msec)

A single significant area of activation was found: ERS at 0-300msec, 15-25Hz, for a cluster in the left medial frontal gyrus extending into the left cingulate gyrus. Therefore, when subjects categorised multicomponent living and nonliving things there was a significant difference in cortical activity for one out or six possible frequency bands. Figure 5.27 illustrates the difference that was found using the voxel level analysis of SnPM.



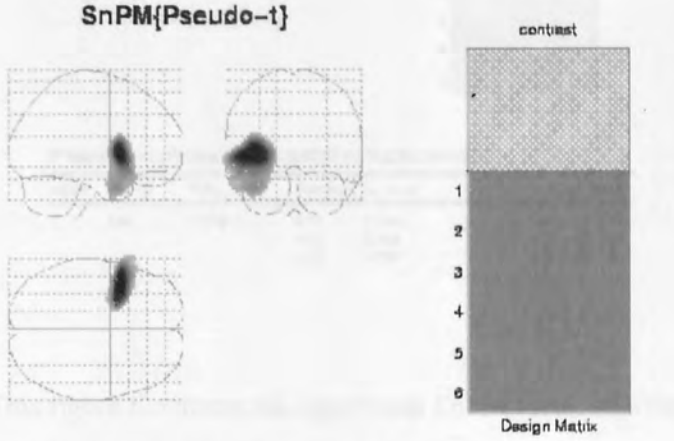
P values & statistics: ./cat0.3HCLv0.3HCNL20-30Hz

region	size {k}	P(K_{max} >= k)	PseudoP(T_{max} >= u)		{x,y,z} mm
1	1108	0.039	5.70	0.051	-6 -6 54
			4.91	0.160	-24 0 33

Figure 5.27. This figure illustrates the significant SnPM result showing ERS at 300msec, 15-25Hz, for a cluster in the left medial frontal gyrus extending into the cingulate gyrus.

ML relative to SL (0-300msec)

A single significant area of activation was found: ERD at 0-300msec, 25-35Hz, for a cluster extending over the left precentral and inferior frontal gyri. Therefore, when subjects categorised living things with different visual configurations there was a significant difference in cortical activity for one out of six possible frequency bands. Figure 5.28 illustrates the difference that was found using the cluster level analysis of SnPM.



P values & statistics: ./cat0.3HCLv0.3LCL25-35Hz

region	size {k}	P{K$_{e}$ >= k}	PseudoP{T$_{e}$ >= u}		{x,y,z} mm
1	1375	0.047	6.00	0.078	-42 12 3
			3.83	0.844	-42 9 -30

Figure 5.28. This figure illustrates the significant SnPM result showing ERS at 300msec, 15-25Hz, for a cluster in the left precentral and inferior frontal gyrus.

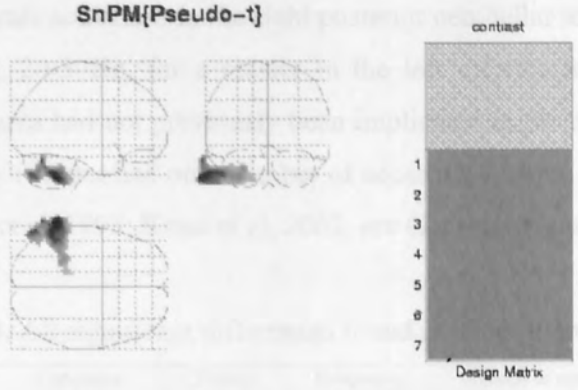
SL relative to SNL (0-300msec)

No significant regions of activity were found in any of the six frequency bands.

SNL relative to MNL (0-300msec)

Two areas of significant activation were found: ERS at 0-300msec, 10-20Hz, for a cluster extending over the left cerebellar tonsil and tuber; and ERD at 0-300msec, 15-25Hz, for a cluster in the left frontal subgyral and extra nuclear regions. Therefore, when subjects categorised nonliving things with different visual configurations there was a significant difference in cortical activity for two out of six frequency bands.

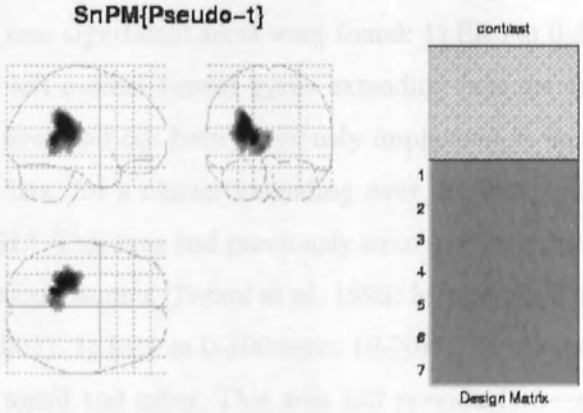
Figures 5.29 and 5.30 illustrate the differences that were found using the cluster level analysis of SnPM.



P values & statistics: ./cat0.3HCNLv0.3LCNL10-20Hz

region	size (k)	P(K_clu >= k)	PseudoP(T_clu >= u)		{x,y,z} mm
1	730	0.016	5.17	0.102	-69 -51 -42
			4.42	0.484	-51 -51 -39
			4.32	0.562	-72 -66 -27

Figure 5.29. This figure illustrates the significant SnPM result showing ERS at 300msec, 10-20Hz, for a cluster in the left cerebellar tonsil and tuber.



P values & statistics: ./cat0.3HCNLv0.3LCNL15-25Hz

region	size (k)	P(K_clu >= k)	PseudoP(T_clu >= u)		{x,y,z} mm
1	957	0.031	4.78	0.363	-18 -48 5
			4.77	0.381	-24 -39 21
			4.05	0.711	-6 -48 0

Figure 5.30. This figure illustrates the significant SnPM result showing ERS at 300msec, 15-25Hz, for a cluster in the left frontal subgyral and extranuclear region.

5.9.3 Summary of results for experiments 4 and 5

Table 5.13 shows the significant areas of the brain that were activated in experiments 4 and 5. When naming, two significant areas were found: 1) ERS at 0-300msec, 15-25Hz, individual voxel activation in the right posterior cerebellar tonsil (ML v SL). 2) ERS at 0-300msec, 20-30Hz, for a cluster in the left inferior frontal gyrus (SL v SNL). The former area had not previously been implicated in the category-specificity literature, however the latter had on a number of occasions (Perani et al, 1995; Martin et al, 1996; Spitzer et al, 1998; Kraut et al, 2002, see General Discussion below).

Table 5.13. All significant differences found in experiments 4 and 5

Experiment	Condition	Timing (sec)	Frequency (Hz)	Area(s) of activity	Moore and Price (1999)
4. Visual configuration (naming)	ML v SL	0.3 v 0.3	15-25	RPCT	RMXS ROT RFFG
4. Visual configuration (naming)	SL v SNL	0.3 v 0.3	20-30	LIFG	BATG BI
5. Visual configuration (categorising)	ML v MNL	0.3 v 0.3	15-25	LMFG and LCG	
5. Visual configuration (categorising)	ML v SL	0.3 v 0.3	25-35	LPCG and LIFG	
5. Visual configuration (categorising)	SNL v MNL	0.3 v 0.3	10-20	LCT and LCTB	
5. Visual configuration (categorising)	SNL v MNL	0.3 v 0.3	15-25	LFSBG and LXN	

When categorising, four significant areas were found: 1) ERS at 0-300msec, 15-25Hz, for a cluster in the left medial frontal gyrus extending into the left cingulate gyrus (ML v MNL). This area had not been previously implicated in the literature. 2) ERD at 0-300msec, 25-35Hz, for a cluster extending over the left precentral and inferior frontal gyri (ML v SL). This area had previously been implicated in Experiment 4 and in a number of previous studies (Perani et al, 1995; Martin et al, 1996; Spitzer et al, 1998; Kraut et al, 2002). 3) ERS at 0-300msec, 10-20Hz, for a cluster extending over the left cerebellum tonsil and tuber. This area had previously been implicated in the Perani et al (1999) study. 4) ERD at 0-300msec, 15-25Hz, for a cluster in the left frontal subgyral and extra nuclear regions (both SNL v MNL). This area had not previously been implicated in the functional imaging literature on category-specificity.

5.10 GENERAL DISCUSSION

In this chapter data was reported from five MEG experiments designed to investigate the neural correlates of category-specific knowledge. The first two experiments examined activity when subjects named items from living and nonliving categories (overtly and covertly) and the third when they categorised the same items as living or nonliving. Overall, there was evidence of a reliable network of cortical activity involved in recognising items from both categories, however, there was no evidence that the recognition of items from living and nonliving categories resulted in areas of the cortex being differentially activated. Experiments 4 and 5 examined the effect of visual configuration on naming and categorising, respectively. There was no consistent evidence that the recognition of visually simple and visually complex objects resulted in areas of the brain being differentially activated, both when the items being recognised were from the same category (e.g. living) or from different ones (living-nonliving). In the following sections, the relationship between the findings from the current set of experiments and from the functional imaging studies outlined in the introduction to this chapter were examined, as were the methodological issues that pertain to the results. Finally, the implications of these data for models of category-specificity were assessed, and future avenues of research considered.

5.10.1 Discussion of Experiments 1-3

Each of the first three experiments identified differences between living and nonliving things, but there was no consistency across the experiments and they failed to produce results that had previously been reported in the functional imaging literature. The only common finding was activation of the right precentral gyrus, as found by Devlin et al (2002) for nonliving relative to living things, however, this was at an uncorrected level of significance ($p<0.001$). Lack of statistical power, coupled with the area not having been previously reported as significant led Devlin et al to conclude it was likely to be the result of a Type I error. In the following section, the functional significance of the four areas found in experiments 1-3 were considered in light of evidence from studies that have implicated these areas and frequencies in related experimental tasks.

Parahippocampal gyrus activity

In Experiment 1 (overt naming) the significant finding of beta band activity in the right parahippocampal gyrus had no corresponding finding in the functional imaging literature on category-specificity. However, Uchida et al (2001) reported beta oscillations in parahippocampal areas and proposed that this area could play a functional role in memory. In terms of the theoretical models of category-specificity outlined in the introduction to this chapter, parahippocampal activity was not one of the predicted areas of activation. However, the present findings suggest that it may have functional significance in terms of a differential involvement in retrieving information related to naming living and nonliving things. Consistent with this, the timing may have been indicative of a semantic retrieval explanation rather than one of perceptual processing because the comparison was made over the whole 700msec epoch. This epoch was used to cover all the components of object naming, not just the perceptual components covered in the 300msec epoch.

Bilateral anterior cingulate activation

In Experiment 2 (covert naming) there was high beta band activity in the anterior cingulate. This area had not previously been found in the functional imaging literature on category-specific knowledge. The anterior cingulate has been implicated in a number of functional roles (e.g. motor control, cognition, arousal, attention), and recent evidence suggests that it is important in translating intentions into actions (Paus, 2001). However, there have not been any reports of high beta band activity associated with this area. None of the theoretical models of category-specificity predicted the involvement of the anterior cingulate in recognising living or nonliving things.

Right precentral and postcentral gyri activation

Also in Experiment 2 there was low gamma band activity in the right post and precentral gyrus. Neither of these areas had previously been implicated in the functional imaging literature for pictures, however, Devlin et al (2002) found the right precentral gyrus was significantly activated for living things compared to nonliving at an uncorrected $p<0.001$ level in a lexical decision task. The precentral gyrus represents the primary motor cortex, and the postcentral gyrus represents primary somatosensory cortex. Both these areas have been associated with alpha and beta band

oscillations during sensorimotor tasks (e.g. Salenius et al, 1997), but gamma activity is not typically found in these areas. However, interestingly, low frequency gamma activity (25-35Hz) was reported in a rhesus monkey study in both the right precentral and postcentral regions during a sensorimotor task (Murthy & Fetz, 1992). In terms of the theoretical models of category-specificity the finding of differential activity in motor areas concurs with the predictions of Warrington and Shallice (1984) who, in their sensory-functional hypothesis, argued that sensory and motor areas would be differentially activated for living and nonliving things, respectively. Consistent with this, the functional significance of the present findings could be related to the aforementioned motor simulation explanation for differences between living and nonliving things. Hence, covertly naming a nonliving object such as a tool may have been sufficient to generate cortical activation with respect to potential action (e.g. Grezes & Decety, 2002, see Section 5.1 and Section 5.10.2).

All significant activity in Experiment 2 resulted from the comparison of the first 300msec post stimulus presentation, suggesting that the living-nonliving differences were related to differences in perceptual processing, rather than later semantic or lexical processing. Again, this concurs with the idea that naming pictures from different categories may activate different areas of cortex associated with their inherent perceptual nature (i.e., motor areas with nonliving things, sensory areas with living things). However, it conflicts with the predictions of Caramazza and Shelton (1998) that any categorical differences should be evident for perceptual *and* semantic processing.

Right superior frontal gyrus activation

In Experiment 3 (categorising) significant activity in the 10-20Hz range was found in the right superior frontal gyrus. Again, this area had not been previously implicated in the literature on category-specificity. Interestingly, activation in right medial and superior frontal gyri has been associated with the establishment in working memory of plans related to intentional behaviour (Clark et al, 2001). This latter finding would be consistent with subjects linking sensory information (pictures) to a particular response (living-nonliving) based on a set of goals (categorise these pictures as living or nonliving), but how this would result in differential activity for living and nonliving things is unclear. Moreover, the difference was observed in the 300msec

comparison, before semantic retrieval processes are postulated to be involved in object categorising (see Kiefer, 2001).

Overall, however, in the first three experiments, there was little evidence to support the theoretical models of category-specificity that advocate the involvement of differentially organised systems for the naming and categorising of living and nonliving things. Three of the four significant findings had no corresponding finding in the literature, and none were replicated across the three experiments. However, before this position can be stated with confidence some methodological issues require consideration (see Section 5.10.3). Prior to this the findings from experiments 4 and 5 are considered.

5.10.2 Discussion of experiments 4 and 5

Experiments 4 and 5 were designed to examine the effects of visual configuration on naming and categorising living and nonliving things. Moore and Price (1999) carried out the same experiment for naming, however, there were no common areas of activity found between the two studies (see Table 5.13). Of the six significant areas presented in Table 5.13, two were consistent with the existing functional imaging literature on category-specificity, however, within the two experiments there were several interesting consistencies.

Cerebellar activity

Perani et al (1999) reported that the left cerebellum was differentially activated for nonliving relative to living things when subjects matched visually presented words (however, this was only at an uncorrected statistical threshold of $p<0.01$). In the present study low beta-band activity (10-20Hz) in left cerebellar regions was found in Experiment 5 (categorising) for the comparison of multicomponent and simple shaped nonliving things. Taken alone, this finding would suggest that the left cerebellum was differentially involved in the processing of different levels of visual complexity, however, the corresponding result from the comparison of living things with different levels of visual complexity failed to reveal any differences in any frequency range. However, in Experiment 4 (naming) beta band activity (15-25Hz) in the right cerebellum was implicated for the comparison of living things with different visual configurations. Therefore, there did appear to be some consistency of activity in the

cerebellum when multicomponent and simple shaped items were compared, albeit in different (naming and categorising) experiments.

The cerebellum has traditionally been described as a co-ordinator of motor actions, and beta band activity in the cerebellum has often been reported as accompanying sensorimotor events (e.g. Babiloni et al, 2002). In terms of the theoretical models of category-specific knowledge, cerebellar activity was not one of the predicted areas of activation. However, the present findings suggest that it may have functional significance in terms of a differential involvement in processing living and nonliving things dependent upon their visual complexity. Here, the left cerebellum was associated with discrimination between nonliving things, and the right cerebellum was associated with discrimination between living things. Some recent related evidence comes from studies designed to investigate the contribution of the cerebellum during visual discrimination tasks (Dupont et al, 1998; Claeys et al, 2003), and visual categorisation tasks that differed in terms of attention (Allen et al, 1997; Rees et al 1997). For instance, Claeys et al (2003) found lateral cerebellar activity when subjects discriminated between different categories (e.g. shades of brown).

Left frontal gyrus and subgyral activation

The left inferior frontal gyrus (Broca's area) was reported in four previous studies all for the activation of nonliving relative to living things (Perani et al, 1995; Martin et al, 1996; Spitzer et al, 1998; Kraut et al, 2002). Evidence for this areas role in recognising nonliving things was supported by data from lesion studies where patients with category-specific impairments for nonliving things typically had left fronto-parietal damage (see Section 1.4.1). It should be noted however that Spitzer et al (1998) found differential activation for living things *and* nonliving things for different subjects (no group analysis was carried out in the Spitzer study). Therefore, activation of left inferior frontal cortex is a (relatively) reliable finding in this literature. In the present set of experiments areas of activity in left frontal regions were found on a number of occasions, these included inferior frontal and precentral gyri, as well as subgyral activation.

The left inferior frontal gyrus was specifically implicated as ERS (20-30Hz) in Experiment 4 (naming) for the comparison of simple shaped living (fruit and

vegetables) and nonliving (tools) things. This finding suggested that there was an effect of category for the naming of simple shaped living and nonliving things that resulted in differential activation of the left inferior frontal cortex. Therefore, the data from Experiment 4 revealed one area of interest in the left inferior frontal gyrus but this was not supported by the remaining comparisons.

Several left frontal areas were found to be significant in Experiment 5 (categorising). The left inferior frontal gyrus was implicated as ERD (25-35Hz) for the comparison of multicomponent (animals) and simple shaped (fruit and vegetables) living things suggesting that there was an effect of visual configuration when subjects categorised. Further support for this was found in the comparison between multicomponent nonliving things (vehicles) and simple shaped nonliving things (tools) where left frontal activation was found in subgyral and extra nuclear regions (an area very close to the inferior gyrus). A significant category effect was also found in Experiment 5 for the comparison of multicomponent living and nonliving things in the left medial frontal region, extending into the cingulate gyrus. Therefore, the data from Experiment 5 revealed a reliable network of activation in left inferior frontal regions (gyral and subgyral) for the recognition of items with different visual configurations regardless of category, and in the left medial (gyral and subgyral) region for the recognition of items from different categories for visually complex items.

In terms of frequency, the significant areas of activity were mainly found in higher bands (beta and lower gamma). Left frontal activation has often been associated with beta and gamma band activity in speech areas during language tasks. In related work, Ihara et al (2003) found significant gamma activity associated with the syntactic processing of function words, and Muller et al (1999) found increased gamma activity (30-50Hz) when subjects processed pictures with different level of emotional content. In terms of the theoretical models of category-specificity, the finding of differential activity in left frontal regions concurs with Warrington and Shallice (1984) who predicted the involvement of motor areas for nonliving things in their sensory-functional hypothesis. In addition, they argued that these differences would be observed in both object naming and categorising tasks, a proposition also supported by the finding of left frontal areas of activation in both experiments 4 and 5. However,

none of the other theoretical models of category-specificity were supported by the present findings (see Section 5.10.4).

One theory that does fit the findings of left inferior frontal activity is the abovementioned mirror-matching hypothesis. It has been well documented that the mirror neuron area F5 in the monkey is the homologue of Broca's area (left inferior frontal gyrus) in humans (e.g. Rizzolatti and Arbib 1998). Indeed, two PET studies have found activation of a mirror-matching system in Broca's area (Grafton et al, 1996; Rizzolatti et al, 1996). Functionally, a difference between Broca's area and F5 is that the former is most commonly thought of as an area for speech, whereas the latter is often considered as an area for hand movements. F5 is somatotopically organised, its dorsal part contains a representation of hand movements (Rizzolatti et al, 1988) and its large ventral part contains a representation of mouth and larynx movement (Gentilucci et al, 1988). Similarly, the motor properties of human Broca's area do not relate only to speech. For example, a PET study showed evidence that Broca's area might also become active during the execution of hand or arm movements (Schlaug et al, 1994), during mental imagery of hand grasping movements (Decety, 1994), and during tasks involving hand mental rotations (Parsons, 1995). Therefore, Broca's activation may be related to actions associated with hand movements such as grasping, or the characteristic movement patterns associated with tool use. Hence, naming or categorising a nonliving object such as a tool may have been sufficient to generate cortical activation in the left inferior frontal gyrus with respect to potential action. However, this theory is unable to explain why in Experiment differential left frontal activation was also found within the same category (both living and nonliving) but for different visual configurations.

For all naming experiments the significant findings were observed in the higher frequency bands (beta and gamma), whereas in the categorising experiments the significant findings tended to be lower in frequency (10-20Hz). This could reflect the functional significance of frequencies in the beta and gamma range in terms of their role in naming compared to categorising. In particular, object naming and categorising use the same perceptual components, but naming requires computation of more semantic features than categorising for identification (see Glaser, 1994). Therefore, it is possible that accessing more detailed semantic information about objects results in

the observed higher frequency band activity. Indeed, there is recent evidence for the functional role of gamma-band activity in complex cognitive processes such as object recognition (e.g. Tallon-Baudry & Bertrand, 1999).

5.10.3 Methodological issues

Although a number of tentative conclusions have been drawn regarding significant areas of activation that differed in terms of category and visual configuration, in the main, the experiments in this chapter failed to reveal significant patterns of cortical activity that corresponded with the previous literature. The conspicuous difference was the lack of activation in the visual cortices, in particular, medial extrastriate cortex (e.g. lingual and fusiform gyri), which have provided some of the most reliable findings in the PET and fMRI studies discussed. Importantly, this deficiency was not only evident in the comparisons between active states (e.g. living and nonliving) but also between active and baseline states.

Firstly, the experimental design was robust because the behavioural data demonstrated that subjects' were able to carry out the task accurately and quickly. Furthermore, the data replicated the reaction time findings in the literature. In Experiment 2 the behavioural data replicated that of Lloyd-Jones and Humphreys (1996) who found that subjects responded faster when naming nonliving compared to living things. In Experiment 3 the behavioural data replicated that of Humphreys et al (1999) who found that subjects were able to make category decisions about living things faster than decisions about nonliving things (see also Riddoch & Humphreys, 1987).

Another methodological issue was whether MEG, and the statistical methods employed to analyse the recorded data, were of sufficient sensitivity to reveal any differences in cortical activity. In each of the first three experiments there were significant differences found between active and baseline states that were reliable across the range of frequencies examined in each experiment, and across the different experiments themselves. Therefore, it would appear that the sensitivity of the equipment used and the power of the statistical analysis employed was not a confounding factor in revealing any differences in cortical activity.

A combination of experimental design and method of analysis may have contributed to a lack of sensitivity in revealing the visual regions involved in recognising items (and perhaps those areas that were specific to different categories). As was previously discussed a limitation of SAM is that perfectly synchronous sources of activity cancel each other out and are therefore difficult to detect. This causes problems analysing data from experiments that examine source activity by means of averaging over hundreds of brief epochs to form a phase-locked response. The shorter the epoch, the greater the probability of finding highly correlated time-course activity from multiple sources. The experimental paradigm employed in the five experiments reported here was designed with two methods of analysis in mind, i.e., dipole fitting and group-SAM. Accordingly, data from each stimulus was averaged over relatively short epochs (2.9secs) in order that both methods of analysis could be used. Dipole fitting was found to be an unreliable technique (see Section 5.5.2), and as a result group-SAM was the method of choice. Perhaps the short epochs used resulted in the synchronisation of early aspects of cortical activity (e.g. during visual processing) and as a result made significant occipital activity difficult to detect.

In future experiments it would be of benefit to change the experimental design to make full use of SAM *or* dipole fitting, rather than attempt to kill two birds with one stone. For SAM, this could be achieved by employing a block-type experiment as is often used in fMRI studies whereby pictures from one category could be presented in a 20 second block, followed by a 20 baseline condition, then another 20 second block of pictures from the other category. Using such a paradigm with SAM would increase the likelihood of elucidating those areas of cortex involved in early visual processing. In accord with this, Singh et al (2002) have demonstrated that SAM analysis allowed MEG experiments to have exactly the same experimental design as corresponding fMRI experiments, and as a result permitted mutual cross-validation of MEG and fMRI studies (Singh et al, 2002).

A further methodological consideration concerns the frequency bands used. It is possible that the range of each frequency band (10Hz) may have been too restrictive, and some significant patterns of activation could have been missed. Therefore, in future experiments it would be of benefit to include all possible frequency band ranges of interest. For instance, a number of studies have brought to light the

important functional role of theta (3-7Hz) activity in cognitive tasks such as recognition memory (e.g. Burgess & Gruzelier, 1997). Moreover, the present experiments only examined the lower end of the gamma band range (30-40Hz). In light of research that has found interesting results in the upper range of the gamma band it would be of interest to expand the range to include these frequencies in future experiments (approximately 30-90Hz). For instance, recent studies have shown activity in the gamma band range during a variety of behavioural states in both human and animal research (see Lee et al, 2003 for a recent review). One influential idea resulting from these studies is that synchronised neuronal firing in the gamma band may reflect the synchronisation of localised neuronal populations, and can be viewed as a candidate for understanding 'neuronal binding', i.e., how distributed brain activities are integrated during specific (sensory and cognitive) processing. Many of the studies that have investigated synchronised gamma band activity used EEG, however, MEG holds some important advantages for recording gamma activity. As previously mentioned, MEG signals are not smeared by intervening tissue conductivity, allowing more sensitivity to local neuronal activation. This makes MEG more suitable to differentiate between simultaneously active cortical areas. Moreover, if future experiments are interested in the coherence between different cortical areas, then MEG benefits over EEG because of possible artefactual effects caused by coherent activity at the recording reference (MEG has reference free recording).

Therefore, in future experiments it would be important to expand the frequency bands used to encompass both the theta band and the upper gamma band range, particularly if the focus of interest was to contribute to exciting recent research into synchronised gamma band activity by examining the processes involved in categorical object recognition and naming. Indeed, in a recent review Basar et al (2001) argued that gamma, alpha, delta, and theta band oscillations are all important with regard to sensory and cognitive functions, and play a role in how different, synchronously firing, areas of the brain communicate functionally.

5.10.4 Implications for cognitive models of category-specificity

The aforementioned methodological considerations demonstrate the importance of interpreting the current findings with caution, and it is with that caveat in mind that the implications for cognitive models of category-specificity are now considered. The

data in this chapter are at odds with accounts of category-specificity that postulate neural segregation for different categories or semantic properties (e.g. the sensory-functional hypothesis), because semantic processing in both the lexical retrieval and semantic categorisation tasks resulted in equivalent cortical activity for living and nonliving things, and for items with different visual configurations (animals, fruit and vegetables, tools, vehicles). In terms of the predictions outlined in Section 5.3.3 the present data found no evidence to support the claims of Caramazza and Shelton (1998) for a tripartite division in the brain between animals, plants and tools at multiple processing levels (perceptual, semantic, lexical). Some evidence was found to support the prediction of Warrington and Shallice (1984) that nonliving things would differentially activate motor areas compared to living things, and this was found to be the case in the picture naming experiments and, as predicted, in categorising experiments as well. Hence, activity was found in motor areas (precentral and postcentral gyrus, left inferior frontal gyrus) however, no evidence was found to support the predictions of Warrington and Shallice (1984) that living things would differentially activate sensory areas (i.e. occipital and temporal regions). The lack of a difference between living and nonliving things in anterior temporal cortex during basic level naming provided evidence against the predictions of Moss and colleagues. Finally, the prediction of Humphreys and Forde (2001) that there would be a neuroanatomical difference between living and nonliving things in more posterior regions than proposed by Moss and colleagues due to living things requiring more 're-activation' of areas involved in early visual processing was not upheld, regardless of task.

Therefore, the results from this chapter support an anatomically distributed account of semantic knowledge that is non-differentiated by category or semantic property. There were a number of related accounts of category-specificity that proposed a non-differentiated organisation of semantic (and pre-semantic) knowledge discussed previously (see Section 1.3) however, while it is relatively straightforward to assess whether or not there is functional segregation in the brain, evaluating the nature of a non-differentiated account like the one proposed here is more difficult. A finding of no specialised systems for living and nonliving things is a null result and only allows for tentative conclusions. Nevertheless, the results from this chapter add to the empirical data outlined in the previous chapters in proposing that category-specific

knowledge is distributed in a unitary system rather than being segregated in distinct subsystems.

Future MEG experiments investigating the neural correlates of category-specific knowledge would find benefit from increasing the number of subjects for group comparisons, which in turn would increase the statistical power, and therefore the likelihood of a significant area of activity being detected. Furthermore, as different methods of analysing the data evolve, and experiments are carried out with differing degrees of success, the choice of analytical method can more readily be determined in conjunction with the experimental design, in order that they complement each other rather than become an *a priori* issue of methodological concern.

5.11 CONCLUSION

In conclusion, the data reported in this chapter suggested that semantic knowledge of living and nonliving things is represented in a distributed, non-differentiated neural system rather than being anatomically segregated in the brain. This claim is compatible with the extant functional imaging literature on category-specificity, which has found little evidence of consistent specialisation for either living or nonliving things. However, it should be noted that the method of analysing MEG data using synthetic aperture mapping (SAM), coupled with the possibility of an unsuitable experimental task design, would need to be resolved before this claim can be substantiated.

CHAPTER 6
GENERAL SUMMARY AND CONCLUSIONS

6.1 INTRODUCTION

In this final chapter the main findings and theoretical implications from each of the four experimental chapters will be summarised and discussed.

6.2 Summary of Chapter 2

The aim of this chapter was to examine the relationship between feature knowledge and category structure by analysing feature norms generated by subjects in a semantic definition experiment. The data was used to assess theories of category-specificity that maintain the importance of different properties (e.g. sensory-functional), for different categories, and to provide a sufficient quantity of feature norms to permit basic-level categories to be considered (e.g. animals, birds, tools, vehicles) as well as the usual higher-level category (living-nonliving). Four feature-based methods of analysis were employed: 1) feature-types, 2) core features, 3) distinctive versus shared features, and 4) feature correlations.

The data revealed a distinction between the types of features generated for living and nonliving things, and for basic-level categories within the living-nonliving classification. For the first time, this was found to be the case when sensory features were compared to functional features for both narrow and wide definitions, and even when sensory features were compared to all nonsensory features. Furthermore, these findings were maintained over three different methods of analyses: 1) all feature-types, 2) core feature-types, and 3) distinctive and shared feature-types. Accordingly, the data revealed that there was a consistent category structure in terms of feature knowledge, and supported the fundamental claim of the S-F hypothesis that semantic knowledge about living and nonliving things is principally encoded in terms of sensory and functional features.

6.3 Summary of Chapter 3

This chapter reported a longitudinal study on a patient DW with a category-specific agnosia for living things. The extent to which his impairment changed over time was evaluated by comparing data collected in 1988 with his performance on the same

tests, using the same stimuli, 12 years later. DW was significantly better at identifying real objects compared to line drawings, his category-specific impairment for living things remained over the 12-year period, and his ability to identify real nonliving objects improved over time but his recognition of real living objects remained at floor. In addition, his ability to access stored visual knowledge for shape declined over time. This latter finding provided support for the proposal of Riddoch et al (1999) that without perceptual input updating or maintaining stored visual knowledge, this information will deteriorate over time. Moreover, it supported an interactive account of visual object recognition (e.g. Ellis & Humphreys, 1999) rather than an account stressing independent perceptual and memorial processes (e.g. Behrmann et al, 1992).

The observed decline in DW's stored visual knowledge had implications for theories of category-specificity. For example, Humphreys et al. (1988) suggested that living things are more structurally similar to one another than nonliving things and identification of living things requires access to more detailed visual information (see Section 1.3.5). This theory predicts that if stored visual knowledge is not updated by visual perception, this will have a greater effect on living compared to nonliving things because the former rely more heavily on visual cues to distinguish a target from competing exemplars (Humphreys et al, 2002). In contrast, for nonliving things, stored functional information, rather than visual knowledge, may be more informative for differentiating between one exemplar and another (Warrington & Shallice, 1984). Consistent with this, DW's ability to draw living things from memory deteriorated more than his ability to draw nonliving things. In addition, when asked to define objects, he recalled fewer visual features of living things at time 2 compared to time 1 but his recall of the visual features of nonliving things remained stable.

The visual properties of nonliving things may also be relatively preserved as a result of privileged links between visual and functional knowledge for these objects. For instance, Moss and colleagues suggested that form-function correlations for living things tend to exist between visual features that are common to many living things (e.g. has legs, has ears) and their biological functions (e.g. can run, can hear). Thus, as visual knowledge declines over time, the interactive links between intact functional properties and visual knowledge may only help to maintain information about visual features that are common to many exemplars. Consistent with this, DW was able to

describe the generic properties of animals (e.g. has legs, has a tail) but he was unable to recall the specific visual attributes of animals (e.g. that a giraffe has long legs, that a pig has a curly tail). Therefore, the decline in his ability to retrieve visual properties of living things compared to nonliving things provided support for accounts that stress the importance of different types of knowledge for differentiating between exemplars from different categories (e.g. Warrington & Shallice, 1984), and the role of form-function correlations in semantic memory (e.g. Moss et al, 1997).

6.4 Summary of Chapter 4

In this chapter local and global processing in object recognition was investigated via two case studies on patients (DW and HJA) with integrative visual agnosia. The objectives were to investigate the nature of both patients' visual recognition impairments and to test if their integrative agnosia could have led directly to their category-specific deficit for living things. The data had implications for theories of category-specificity and also for understanding the role of local and global processing in visual object recognition.

In the selective attention experiment control subjects were significantly faster at processing local information and showed a reliable local-to-global interference effect. DW and HJA were also significantly faster at processing local information, however, they did not show a local-to-global interference effect. This was difficult to explain in terms of an attentional spotlight theory and, overall, the data was most consistent with the suggestion that local processing, global processing and the integration of this information are mediated by separate mechanisms (Lamb & Robertson, 1990).

In the divided attention experiment, interference effects were found for both DW and HJA. To account for the different pattern of results in the selective and divided attention experiments, it was suggested that DW showed an abnormal attentional bias to local features, and that HJA had a perceptual problem integrating local and global information. When DW was forced to divide his attention, he was able to simultaneously process and integrate local and global information. Similarly, HJA was able to simultaneously process local and global information when forced to divide his attention, however, he remained impaired when the task required him to integrate that information. Therefore, the data demonstrated that this relatively subtle

difference in performance on a task of local and global processing nevertheless resulted in the same object recognition deficit for both patients, i.e., a category-specific impairment for living things.

6.5 Summary of Chapter 5

The aim of this chapter was to investigate the neural correlates of category-specific knowledge using MEG. There was no consistent evidence that the recognition of items from living and nonliving categories resulted in activation of different cortical areas. Furthermore, there was no consistent evidence that the recognition of visually simple and visually complex objects resulted in areas of the brain being differentially activated, both when the items being recognised were from the same category (e.g. living) or from different ones (living-nonliving). Hence, the experiments in this chapter failed to reveal significant patterns of cortical activity that corresponded with the previous literature.

The conspicuous difference was the lack of activation in the visual cortices, in particular, medial extrastriate cortex (e.g. lingual and fusiform gyri), which have provided the most reliable findings in PET and fMRI studies. Importantly, this deficiency was not only evident in the comparisons between active states (e.g. living and nonliving) but also between active and baseline states, suggesting that a combination of experimental design and method of analysis may have contributed to a lack of sensitivity in revealing the visual regions involved in recognising items (and perhaps those areas that were specific to different categories).

The implications for models of category-specificity were discussed with these methodological considerations in mind. The results were at odds with accounts of category-specificity that postulate neural segregation for different categories or semantic properties (e.g. the sensory-functional hypothesis), because semantic processing in both the lexical retrieval and semantic categorisation tasks resulted in equivalent cortical activity for living and nonliving things, and for items with different visual configurations (animals, fruit and vegetables, tools, vehicles). There was no evidence to support the claims of Caramazza and Shelton (1998) that there is a tripartite division in the brain between animals, plants and tools at multiple processing levels (perceptual, semantic, lexical). Neither was there evidence found to support the

predictions of Warrington and Shallice (1984) that living and nonliving things differentially activated sensory and motor areas, respectively, in both naming and categorising tasks. The lack of a difference between living and nonliving things in anterior temporal cortex during basic level naming provided evidence against the predictions of Moss and colleagues. Finally, the prediction of Humphreys and Forde (2001) of a neuroanatomical difference between living and nonliving things in more posterior regions than proposed by Moss and colleagues due to re-entrant activation of visual processing areas when living things were identified, was not substantiated.

Therefore, the results from this chapter supported an anatomically distributed account of semantic knowledge that is non-differentiated by category or semantic property. However, this proposition was based on a null finding, and as a result the conclusion is at best tentative. In retrospect, it is possible that the new method of analysing MEG data using synthetic aperture mapping (SAM) was not well matched to the experimental design. Therefore, future MEG studies of category-specificity would benefit from determining the analytical method in conjunction with the experimental design, in order that they complement each other rather than become an *a priori* issue of methodological concern.

6.6 CONCLUSION

In conclusion, this thesis has presented a range of empirical data with important consequences for current understanding of the phenomenon of category-specificity. In the normal subjects definition experiment, evidence was found that semantic knowledge about living and nonliving things is principally encoded in terms of sensory and functional features, respectively. In the two case-study chapters that followed, evidence was found supporting the view that category-specific impairments can arise from damage to a pre-semantic system, rather than the assumption often made in the literature that the system involved must be semantic. In the final experimental chapter, rather than finding evidence for the involvement of specific brain areas for different object categories, a number of MEG experiments produced data that seemed to indicate that naming and categorising living and nonliving things involved a non-differentiated neural system. However, it should be noted in parenthesis that a strong interpretation of this latter finding was constrained by a possible methodological conflict between the experimental design and method of

analysis. Therefore, in conclusion, this thesis has extended our current understanding of the processes and organising principles of category-specificity, by drawing together related evidence about stored knowledge of living and nonliving things, through the application of different but complementary research methods.

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APPENDIX A
CLASSIFICATION FOR NORMAL SUBJECT FEATURES EXPERIMENT

ANIMALS (35)

1) ALLIGATOR		
Reptile	16	superordinate
Dangerous/vicious	14	other
Lives in rivers/lakes/water	12	other
Large	11	visual
Long	9	visual
Scaly	9	tactile
Long tail	9	visual
Snout	8	visual
Large teeth	8	visual
Like a crocodile	7	like a
Animal	5	superordinate
Hot climate	5	other
Large mouth	3	visual
4 legs	2	visual
Crawls around	2	associated action
Snapping jaw	2	associated action
Man eating	2	other
Short legs	2	visual
Brown	2	visual
Carnivore	2	superordinate
2) CAMEL		
1 or 2 humps	20	visual
Animal	19	superordinate
Go without water for long time	12	other
Large	10	visual
Lives in desert	10	other
4 legs	9	visual
Carries humans	6	functional
Dromedary	2	other
Long legs	2	visual
Skin covers feet to stop sinking	2	other
3) CAT		
Animal	19	superordinate
4 legs	16	visual
Furry/hairy	14	tactile
Kept as pets	11	other
Has claws	10	visual
Long tail	10	visual
Various breeds	10	other
Different colours/markings	10	visual
Meowing sound	10	auditory
Purring sound	8	auditory
Whiskers	6	visual
Hissing sound	5	auditory
Feline family	4	superordinate
Sharp teeth	4	visual
Popular	3	other
Agile	3	other
Sharp claws	3	tactile
Pointy ears	2	visual

Different sizes	2	visual
Worshipped by Egyptians	2	other
Black cats unlucky/lucky	2	other
4) COW		
Milk	15	functional
Lives on farm/farmed	10	other
Meat	9	functional
Animal	8	superordinate
Eats grass	8	other
Large	8	visual
4 legs	8	visual
Mammal	6	superordinate
Black and white	4	visual
Moos	4	auditory
Female	2	other
Ruminant	2	other
Docile	2	other
Udders	2	visual
5) DEER		
Animal	13	superordinate
Antlers	11	visual
4 legs	10	visual
Lives in forest/woodland	8	other
Mammal	8	superordinate
Timid	3	other
Wild	3	other
Hunted	3	other
Large	2	visual
Stags	2	other
Bambi	2	other
Brown	2	visual
Herbivores	2	superordinate
Eaten	2	functional
Venison	2	functional
6) DOG		
4 legs	16	visual
Animal	12	superordinate
Furry/hairy	12	tactile
Barks/yaps	10	auditory
Variety of breeds	9	other
Domestic pet	7	other
Man's best friend	7	other
Tail	6	visual
Variety of sizes	5	visual
Mammal	5	superordinate
Sharp teeth	2	tactile
Wild	2	other
Wags tail	2	visual
7) DONKEY		
Like a horse	14	like a
Animal	10	superordinate
Big/large/long ears	9	visual
4 legs	9	visual
Fur	6	tactile
Mammal	6	superordinate
Grey	5	visual

Tail	4	visual
Brown	4	visual
Used/ridden on beaches	3	functional
Large	3	visual
Neigh	2	auditory
Smaller than horse	2	visual
8) ELEPHANT		
Trunk	20	visual
Large	17	visual
Grey	14	visual
African/Indian	14	other
Large ears	14	visual
Animal	12	superordinate
Mammal	7	superordinate
Tusks	3	visual
Extinct (in South Africa)	2	other
Wrinkly	2	visual
Trunk used to find food	2	other
Afraid of mice	2	other
Safari	2	other
9) FISH		
Lives in sea/water/aquatic	16	other
Gills	13	visual
Animal/creature	13	superordinate
Swims	10	associated action
Fins	9	visual
Breathes	8	other
Edible	8	functional
Scales	7	visual
Kept as pets	4	other
Good with chips	2	other
10) FOX		
Red	11	visual
Dog-like	10	like a
Bushy tail	10	tactile
Animal	9	superordinate
Mammal	7	superordinate
Predator	7	other
Lives in woodland/fields/count	8	other
Hunted	5	other
4 legs	3	visual
Orange	3	visual
Furry/hairy	3	tactile
Long/large tail	3	visual
Wild	3	other
Urban	3	other
Carnivore	3	superordinate
Pest	2	other
Cunning	2	other
Lives in den	2	other
Nocturnal	2	other
11) FROG		
Amphibian	12	superordinate
Lives in ponds/swamps/water	12	other
Green	10	visual
Hops/jumps/leaps	10	associated action

Small	10	visual
Animal/creature	7	superordinate
Croaking/ribbit sound	6	auditory
4 legs	3	visual
Variety of colours	3	visual
Eat insects/flies with tongue	3	associated action
Slimy	2	tactile
Like/related to toads	2	like a
Two large eyes	2	visual
Come from tadpoles	2	other
Powerful back legs	2	other
Reptile	2	superordinate
Lays eggs/frogspawn	2	other

12) GIRAFFE

Long neck	19	visual
Animal	19	superordinate
Very tall	17	visual
4 legs	16	visual
Long legs	11	visual
Spotted/patchy colouring	11	visual
Eats leaves from trees	10	associated action
Coloured skin	8	visual
Yellow and brown colour	7	visual
Graze at top of trees	6	associated action
Africa	6	other
Tail	5	visual
Wild	4	other
Stump horns	4	visual
Herbivore	4	superordinate
Has hooves	2	visual
Lives in zoos	2	other

13) GOAT

Animal	18	superordinate
4 legs	12	visual
Cheese	11	functional
Milk	10	functional
Horns	10	visual
Beard	9	visual
Aggressive/bad temper	6	other
White	5	visual
Bleating sound	4	auditory
Mountain type	2	other
Short tail	2	visual

14) GORILLA

Hairy/furry	20	visual
Large	17	visual
Like a human	11	like a
Black/dark colour	9	visual
Animal	7	superordinate
Lives in jungle/rainforest	7	other
Mammal	6	superordinate
Ape family	4	superordinate
Lives in wilderness	3	other
4 legs	3	visual
Move in packs	3	other
Primate	3	superordinate
Protected/endangered species	2	other

Swings through trees	2	associated action
15) HORSE		
Animal	16	superordinate
Tail	13	visual
4 legs	12	visual
Ridden by humans	11	functional
Mane	9	visual
Used for racing	7	functional
Large/big	7	visual
Pull/drive carts	6	functional
Hooves	5	visual
Herbivores	5	other
Various colours	3	visual
Various sizes	3	visual
Long face	3	visual
Shown	2	other
Various breeds	2	other
Kept as pets	2	other
Neighing noise	2	auditory
Used for jumping	2	functional
Eat oats	2	other
16) KANGAROO		
Pouch	17	visual
Australian	16	other
Jumps/hops/bounces	13	associated action
Animal	9	superordinate
Mammal	7	superordinate
Strong legs	5	other
Marsupial	4	superordinate
Large	4	visual
Large/long ears	3	visual
Brown	2	visual
2 legs	2	visual
Floppy ears	2	visual
17) LEOPARD		
Black spots	17	visual
Cat family	16	superordinate
Wild	8	other
Golden	5	visual
Animal	5	superordinate
Tail	4	visual
Hunter/predator	4	other
Very fast	3	other
Africa	3	other
4 legs	3	visual
Mammal	2	superordinate
Yellow and black fur	2	visual
18) LION		
Mane	16	visual
Animal	13	superordinate
Cat (big)	12	superordinate
Roaring noise	10	auditory
Sharp teeth	7	tactile
4 legs	6	visual
Large	6	visual
Sharp claws	6	tactile

Tail	6	visual
Dangerous/vicious	6	other
King of the jungle	5	other
Hairy/furry	4	tactile
Carnivore	4	superordinate
Beige/golden colour	4	visual
In prides	2	other
Predator	2	other

19) LOBSTER

Eaten/food	13	functional
Live in sea/water	13	other
Crustacean	8	superordinate
Pincers	7	visual
Red	6	visual
Large	6	visual
Shell fish	5	superordinate
Delicacy	4	other
Animal/creature	4	superordinate
Claws	3	visual
Orange	3	visual
Hard shell	3	tactile
Cook it	3	other
Like a crab	2	like a

20) MONKEY

Animal	17	superordinate
Swings	12	associated action
Climbs	10	associated action
Lives in the jungle	7	other
Similar to man	6	like a
Eat bananas/vegetation	9	other
Wild	4	other
2 legs	3	visual
2 arms	3	visual
Found in zoo	3	other
Brown skin	3	visual
Hairy/furry	3	tactile
Long tail	2	visual
Nearest intelligence to man	2	other

21) MOUSE

Small	19	visual
Rodent	11	superordinate
Long tail	10	visual
Animal	10	superordinate
Eat cheese	10	associated action
Squeaks	5	auditory
Furry	5	tactile
Common	3	other
Pest	3	other
Grey	3	visual
Whiskers	3	visual
Cats chase them	2	other
Mammal	2	superordinate
Found in houses	2	other
Brown	2	visual

22) PIG

Animal	19	superordinate

Pink	16	visual
4 legs	9	visual
Used for meat	9	functional
Farmyard	8	other
Snout	8	visual
Curly tail	7	visual
Ham	2	functional
Pork	2	functional
Grunting noises	2	auditory
23) RABBIT		
Long ears	15	visual
Small/Little	14	visual
Furry/hairy/fluffy	13	tactile
Animal	9	superordinate
Can be pet	9	other
Mammal	8	superordinate
Wild	7	other
Hops	5	associated action
Small tail	4	visual
Live burrow	3	other
Fluffy tail	3	tactile
Large hind legs	3	visual
Floppy ears	2	visual
Whiskers	2	visual
Twitch nose	2	associated action
Various species/breeds	2	other
4 legs	2	visual
24) RACCOON		
Animal	11	superordinate
Furry/hairy	10	tactile
Mammal	8	superordinate
Small	7	visual
Grey/white	6	visual
Lives in trees/woods/forest	6	other
4 legs	5	visual
Fluffy/bushy tail	4	tactile
Long tail	4	visual
Stripy	3	visual
Lives in America	3	other
Raid bins	3	other
Striped tail	2	visual
25) RHINO		
Large/very big	20	visual
Horned	17	visual
Animal	12	superordinate
Grey	10	visual
Tough/thick skin	10	tactile
Lives in wild	9	other
Found in Africa/African	11	other
Mammal	6	superordinate
Dangerous/vicious	3	other
Found in hot countries	3	other
Black	2	visual
White	2	visual
26) SEAHORSE		
Lives in the sea	16	other

Animal	12	superordinate
Curly/curved tail	11	visual
Horse head	6	visual
Small	6	visual
Fish	5	superordinate
Swims	3	associated action
Swirly shape	2	visual
Upright	2	visual
Like a horse	2	like a

27) SEAL (18)

Live in water/sea	16	other
Mammal	14	superordinate
Grey	6	visual
Animal	5	superordinate
Flippers	5	visual
Swim	4	associated action
Tail	4	visual
Arctic	3	other
Large/Big	3	visual
Live land too	3	other
Small	2	visual
Catch fish	2	associated action
Cute/adorable	2	other
Thick fur	2	tactile

28) SHEEP

Animal	16	superordinate
Wool	16	functional
Farm	11	other
4 legs	8	visual
Meat	6	functional
White	4	visual
Furry	2	tactile
Mammal	2	superordinate
Thin legs	2	visual
Black	2	visual
Baas	2	auditory
Welsh	2	other
Lamb	2	other

29) SKUNK (19)

Expels strong smell	17	taste/smell
Animal	13	superordinate
Black and white	12	visual
Large/long tail	7	visual
American	6	other
Deterrent/defence mechanism	4	associated action
4 legs	4	visual
Small	4	visual
Mammal	4	superordinate
Fluffy/bushy tail	3	tactile
Distinctive stripe	2	visual

30) SNAKE

Reptile	18	superordinate
Limbless	12	visual
Long	9	visual
Poisonous	9	other
Thin	7	visual

Slithers/slides	6	associated action
Scaly skin	5	tactile
Cold blood	3	other
Various lengths	3	visual
Different types	3	visual
Cylindrical	2	visual
Dangerous	2	other
Fork tongue	2	visual
Sheds skin	2	associated action
Eat large animal	2	associated action
Animal	2	superordinate
Green	2	visual
Various colours	2	visual

31) SNAIL

Shell	18	visual
Animal/creature	10	superordinate
Like a slug	9	like a
Small	8	visual
Slow	5	other
House on back	5	other
Insect	3	superordinate
Shell for shelter/protection	3	other
Slimey trail	3	tactile
Mollusc	2	superordinate
Head sticks out	2	visual
Spiral/curved shape shell	2	visual

32) SQUIRREL

Eat acorns/nuts	14	associated action
Animal	13	superordinate
Bushy tail	13	tactile
Live in trees/wood	11	other
Small	11	visual
Grey	6	visual
Red	6	visual
Store nuts	5	associated action
Furry	5	tactile
Rodent	4	superordinate
Hibernates	4	associated action
English/British	3	other

33) TIGER

Big cat	16	superordinate
Black and orange stripes	14	visual
Large	11	visual
Animal	11	superordinate
Asia	10	other
Wild	9	other
Africa	8	other
Yellow	5	visual
Ferocious	5	other
Jungle	4	other
Predator	2	other
Mammal	2	superordinate
Lion size	2	visual
Roars	2	auditory
Furry	2	tactile
Carnivore	2	superordinate

34) TURTLE		
Shell	15	visual
Lives water/sea	15	other
Animal/creature	10	superordinate
Green	6	visual
Swims	6	associated action
Live on land	5	other
Reptile	5	superordinate
4 legs	3	visual
Brown	3	visual
Like tortoise	3	like a
Very slow	2	associated action
Large	2	visual
Goes on beach	2	other
Lays egg	2	associated action
35) ZEBRA		
Black and white stripes	20	visual
Like a horse	19	like a
Animal	13	superordinate
Wild	7	other
Large	5	visual
Africa	5	other
4 legs	5	visual
In herds	2	other
Short mane	2	visual
Mammals	2	superordinate
Fur/hair	2	tactile
Tail	2	visual

BIRDS (9)

36) CHICKEN		
Eaten by humans	16	functional
Bird	13	superordinate
Lays eggs	12	associated action
Has feathers	9	visual
Has wings	5	visual
Found in farms	4	other
Flightless	4	other
2 legs	3	visual
Animal	3	superordinate
Clucking sound	3	auditory
Struts/walks around	2	associated action
Eggs are eaten	2	functional
Small	2	visual
Poultry	2	superordinate
Beak	2	visual
Bred/kept by humans	2	functional
Can fly to some extent	2	associated action
37) DUCK		
Bird	15	superordinate
Live near water	12	other
Bill/beak	8	visual
Quacks	8	auditory
Webbed feet	7	visual
Animal	6	superordinate
Swims	5	associated action

Feathers	5	visual
Many breeds	3	other
Many colours	2	visual
Wings	2	visual
Small	2	visual
Brown	2	visual
Flies	2	associated action

38) EAGLE

Bird (of prey)	17	superordinate
Large	9	visual
Predator	8	other
Associated with America	4	other
Rare	4	other
Wings	3	visual
Flies	2	associated action
Large beak	2	visual
Carnivore	2	superordinate
Golden	2	visual

39) OSTRICH

Bird	18	superordinate
Cannot fly	15	other
Large	12	visual
Large/long neck	9	visual
Quick/fast runner	6	associated action
Buries head in ground	5	associated action
Large/long limbs	4	visual
Lays big eggs	4	associated action
Has feathers	4	visual
2 legs	3	visual
2 wings	2	visual
Animal/creature	2	superordinate

40) OWL

Bird (of prey)	16	superordinate
Nocturnal	15	other
Big eyes	8	visual
Move head 360°	7	associated action
Predator	6	other
Twit-twoo sound	5	auditory
Feathers	3	visual
Various types	3	visual
Wisdom	3	other
Large	2	visual
Brown	2	visual
White	2	visual
Good vision	2	other
Wild	2	other

41) PEACOCK

Bird	17	superordinate
Beautiful feathers	14	visual
Tail	8	visual
Feathers fanned out	7	associated action
Multicoloured	7	visual
Large	6	visual
Feathers used to attract mate	5	other
Display	3	visual
Plumage	3	visual

Beak	3	visual
Green	2	visual
Long neck	2	visual
Distinctive	2	other
42) PENGUIN		
Black and white	12	visual
Bird	8	superordinate
Flightless	7	other
Swims	6	associated action
Eats fish	4	associated action
Cold	4	other
Arctic	3	other
Antarctica	2	other
North/south pole	2	other
Animal	2	superordinate
Webbed feet	2	visual
43) ROOSTER		
Male hen	12	other
Crows in morning	10	associated action
Bird	8	superordinate
Farmyard animal	6	superordinate
Feathered	5	visual
Cockerel	3	other
Beak	3	visual
Creature	3	superordinate
'cock-a-doodle-do'	2	auditory
44) SWAN		
White	20	visual
Bird	15	superordinate
Large	12	visual
Long neck	9	visual
Live near water	7	other
Attractive/beautiful	7	visual
Black	5	visual
Webbed feet	5	visual
Vicious/dangerous	5	other
Swims	4	associated action
Beak	3	visual
Can fly	3	associated action
Property of crown/queen	3	other
Feathers	2	visual

BODY PARTS (13)

45) ARM		
Body part	11	superordinate
Hand on end	10	other
Attached to shoulder	7	other
Connect hand to body	7	functional
Limb	6	superordinate
2 of them	6	visual
Upper	4	other
Elbow	3	other
Use things	2	other
Joint	2	other
46) EAR		

Hear with it	16	functional
Side of head	13	visual
2 of them	6	visual
Body part	6	superordinate
Pick up soundwaves	5	functional
Pierced	4	visual
Cartilage	2	other
Ear drum	2	other

47) EYE

Used for seeing	18	functional
On face /head	10	other
Body part	6	superordinate
Sphere/round shape	4	visual
Part of a pair	4	other
Has an iris	4	visual
Has a pupil	3	visual
Sense organs/senses	3	other
Blue	2	visual
Green	2	visual
Brown	2	visual
All pupils black	2	visual
Different colours	2	visual

48) FINGER

On hand	14	other
Hold object	9	functional
Digit	6	other
4 of them	6	visual
Thumb	5	visual
Nail	4	visual
Body part	3	superordinate
Long	3	visual
Thin	3	visual
10 of them	2	visual
Extension	2	other
Bones/joint	2	other

49) FOOT

End of leg	16	other
Walk on it	13	functional
Body part	9	superordinate
5 toes	7	visual
2 of them	4	visual
Human	3	other
Balance	3	other
Stand on it	3	functional
Shoe/sock	2	other

50) HAIR

On head	14	other
On body	10	other
Different colours	7	visual
Warm/protective	4	functional
Dead cells	3	other
Mammals	3	other
Curly/straight	3	visual
Root/follicle	2	other
Multiple strands	2	visual
Organic	2	other

Fine	2	other
51) HAND		
On end of arm	16	other
Five/four fingers/digits	15	visual
Used to grab/hold/grasp	12	functional
Thumb	6	visual
Used to feel/touch	4	functional
Humans	4	other
A pair	3	other
Five fingernails	3	visual
Fit in glove	2	other
Palm	2	visual
52) HEART		
Pump blood	18	functional
Vital organ	11	superordinate
Muscle	4	superordinate
Body part	3	superordinate
Love symbol	2	other
Keep alive	2	functional
4 chambers	2	visual
Size of fist	2	visual
53) LEG		
Used to walk/stand on	13	functional
Body part	8	superordinate
Limb	6	superordinate
Attach body to foot	4	other
Long	4	visual
Knee joint	4	other
Mammals	3	other
Lower	3	other
Support body	2	functional
2 legs	2	visual
Thin	2	visual
Hip	2	other
Ankle	2	other
54) LIPS		
Mouth	13	other
On face	11	other
Kiss with	10	associated action
Red/pink	6	visual
Moves to eat/talk	5	functional
Flesh	3	visual
Painted by women	3	other
Body part	2	superordinate
In pairs	2	visual
Protect teeth	2	functional
55) NOSE		
Smell	16	functional
On face	15	other
Central/middle	12	visual
Organ	4	superordinate
Breathe	5	functional
Body part	3	superordinate
2 nostrils	5	visual
Sticks out	4	visual

Sense	3	other
Many shapes	2	visual
Many sizes	2	visual

56) THUMB

On hand	16	other
Digit	9	other
Hold things	7	functional
Nail in it	5	visual
Shorter finger	5	visual
Jointed	3	other
First finger	2	other

57) TOE

On end of foot	16	other
Five on each foot/ten of them	9	visual
Helps balance	8	functional
Nail on surface	6	visual
Part of the body	4	superordinate
Have a big one	3	visual
Painted nails	2	visual
Digits	2	other

CLOTHING (21)

58) BELT

Tied/wrapped around waist	19	associated action
Holds up trousers/shorts/skirts	18	functional
Metal buckle	17	visual
Number of holes in it	12	visual
Long	10	visual
Made of leather	10	visual
Strip of material	6	visual
Thin	4	visual
Plastic	4	visual
Decorative	3	other
Item of clothing	2	superordinate
Used for punishment	2	functional

59) BLOUSE

Worn by females	17	other
Buttons on front	11	visual
Item/article/piece of clothing	7	superordinate
Long/short sleeves	6	visual
Collars	5	visual
Many colours	4	visual
Different sizes	3	visual
Upper	3	other
Worn over torso/top of body	3	other
Like a shirt	2	like a

60) BOOT

Worn on foot/footwear	15	other
Cover ankle	8	other
Item of clothing	5	superordinate
Shoe	4	superordinate
Laces	4	visual
Protection	3	other
Sole	3	visual
Walking	2	other

Leg	2	other
Zip	2	visual
Leather	2	visual
61) CAP		
Placed/worn on head	15	other
Item/article of clothing	6	superordinate
Peaked, flat bit	5	visual
Decorative/fashion	4	other
Type of hat	4	superordinate
Protection	3	functional
Sporty	3	other
62) COAT		
Item of clothing	12	superordinate
Worn in/protects against cold	12	other
Worn to keep warm	11	functional
Worn as outer garment	8	other
Worn over/protects clothes	4	other
Worn to keep dry	4	functional
Has sleeves	3	visual
Covers arms	3	other
Many shapes and sizes	2	visual
Many colours	2	visual
Button-up	2	visual
Zip-up	2	visual
Fashion garment	2	superordinate
Front fastening	2	other
63) DRESS		
Item of clothing	17	superordinate
Worn by females	17	other
Covers from shoulders to knee/ calf/thigh/ankle	12	other
Various styles	9	visual
Different lengths	9	visual
Many colours	7	visual
Many sizes	7	visual
Top attached/joined to bottom	6	visual
Long piece of material	5	visual
64) GLOVE		
Clothing for hand	19	functional
Covering/warmth/protection for hand	17	functional
Five fingers/finger parts	6	visual
Used during cold weather	4	other
Woollen	2	visual
Snug/close fitting	2	other
Like mittens	2	like a
Many colours	2	visual
Worn as fashion/appearance	2	other
To keep hands clean	2	functional
65) HAT		
Worn on the head	19	other
Item/article of clothing	17	superordinate
Fashion accessory	10	other
Many styles	10	visual
Different colours	9	visual

Used to keep the sun out	8	functional
Used to keep the head warm	8	functional
Many materials	6	visual
Many shapes	4	visual
Unisex	4	other
Piece of a uniform	2	other
66)JACKET		
Item of clothing	14	superordinate
Wear over clothes	12	other
Warmth	10	functional
Outdoor	8	other
Upper body	6	other
Protection	2	functional
Rain	2	other
Hood	2	visual
Sleeves	2	visual
Buttons	2	visual
Zips	2	visual
Lightweight	2	other
67) MITTEN		
No fingers	12	visual
Worn on hands	11	other
Like a glove	11	like a
Used to keep warm	10	functional
Worn in winter/cold weather	7	other
Space for thumb	6	visual
Clothing	5	superordinate
Child wears them	4	other
Woollen	3	visual
String attached	2	visual
68) NECKLACE		
Wear on neck	18	other
Item of jewellery	15	superordinate
Decorative	3	other
Silver	2	visual
Gold	2	visual
Pearl	2	visual
Accessory	2	other
Female	2	other
69) RING		
Worn on fingers	17	other
Item/piece of jewellery	12	superordinate
Metal	9	visual
Round/circular	8	visual
Gold	6	visual
Indicate marriage	4	other
Silver	4	visual
Hole in centre	3	visual
Plastic	3	visual
Decorative	3	other
Stones	2	other
70) SHIRT		
Covers/worn on upper body	17	other
Item of clothing	16	superordinate
Buttons on front	14	visual

Sleeves (long/short)	9	visual
Collar	8	visual
Unisex	6	other
Various materials	5	visual
Cuffs	4	visual
Worn with tie and suit	3	other
Male equivalent of a blouse	2	like a
Various sizes/shapes	2	visual
Buttons for opening/fastening	2	other
Various colours	2	visual

71) SHOE

Worn on feet	13	other
Protective	8	functional
Item of clothing/footwear	9	superordinate
Leather	7	visual
Laces	5	visual
Different sizes/shapes	5	visual
Buckles	4	visual
Sole	3	visual
Keep feet dry/warm	3	functional
Heel	3	visual
Plastic	3	visual
Walking	3	associated action
Weather	2	other
Velcro	2	visual

72) SKIRT

Clothing	20	superordinate
Worn by women	14	other
Covers lower body	14	functional
Long	5	visual
Short	5	visual
Material	4	visual
Garment	2	superordinate
Legless	2	visual
Worn by men	2	other
Around waist	2	other

73) SOCK

Worn on foot	16	other
Item of clothing	12	superordinate
Keep feet warm	8	functional
Cotton	4	visual
Pairs	3	other
Different colours	3	visual
Worn under shoe	3	other
Wool	3	visual
Ankle	3	other
Protect feet	2	functional
Tube-like	2	like a

74) SWEATER

Item of clothing	15	superordinate
Upper body	11	other
Warm	9	other
Wool	5	visual
Like a jumper	5	like a
Long sleeves	3	visual
Sport	3	other

Variety of colours	2	visual
Fuzzy	2	tactile
Material	2	other
75) TIE		
Item of clothing	18	superordinate
Worn around the neck	17	other
Worn by men/boys/women	15	other
Tied in a knot	14	associated action
Goes around collar of shirt	11	other
Long	8	visual
Many styles	6	visual
Hangs down to the waist	5	other
Variety of colours	4	visual
Many designs	3	other
Part of uniform	2	other
Silk	2	visual
76) TROUSERS		
Used to cover legs/waist down/ lower body	16	functional
Item of clothing	14	superordinate
Two leg parts/shapes	8	visual
Unisex	6	other
Different types/styles	5	other
Different colours	5	visual
Different materials	5	visual
Different sizes	2	visual
Worn casually or formally	2	other
77) WAISTCOAT		
Item/article of clothing	14	superordinate
Sleeveless/no arms	13	visual
Worn as part of suit/uniform	8	other
Like a jacket	6	like a
Smart/formal	6	other
Has buttons	5	visual
Worn over shirt	4	other
Worn for snooker	2	other
Usually worn by men	2	other
Worn under jacket	2	visual
78) WATCH		
Tell time	18	functional
Wrist	18	visual
Item/object	9	superordinate
Face	3	visual
Strap	3	visual
Digital	2	other
FRUIT & VEGETABLES (22)		
79) APPLE		
Fruit	20	superordinate
Green	13	visual
Red	12	visual
Grow on trees	10	other
Round	9	visual
Different types	4	other
Pips/seeds	7	visual

Orchard	3	other
Yellow	3	visual
Juicy	2	taste/smell
Crispy/crunchy	4	tactile
Eat raw	2	other
Core	2	visual

80) ARTICHOKE

Vegetable	18	superordinate
Edible/eaten/used as food	7	functional
Green	6	visual
Has heart inside	3	visual
Small	2	visual
Fruit	2	other

81) ASPARAGUS

Vegetable	19	superordinate
Green	13	visual
Long	7	visual
Thin	5	visual
Tips	4	visual
Delicacy	3	other
Eaten	2	functional
With butter	2	other
Stalk	2	visual
Expensive	2	other

82) BANANA

Fruit	20	superordinate
Yellow	20	visual
Curved/bent	11	visual
Peel off skin (before eating)	8	associated action
Contents eaten/edible	5	functional
Long	5	visual
Grow in tropical/hot places	4	other
Grow on trees	3	other
Green when unripe	2	visual
Tastes sweet	2	taste
Nutritious/good to eat	2	other
Used in puddings/dessert	2	functional

83) CARROT

Orange	20	visual
Vegetable	19	superordinate
Eaten raw	14	other
Cooked	12	other
Thin	7	visual
Long	7	visual
Root vegetable	6	superordinate
Contains vitamin A	6	other
Make you see in the dark	6	other
Tapered	5	visual
Grow in the ground	4	other
Associated with rabbits	3	other

84) CELERY

Vegetable	16	superordinate
Green (light)	14	visual
Food (salad food)	12	functional
Long	10	visual

High water content	8	other
Like a stick	7	like a
Crunchy	5	tactile
Eat raw	4	other
Eat cooked	4	other
Ridged	3	tactile
Leafy top	2	visual
Bland taste	2	taste/smell

85) CHERRY

Fruit	19	superordinate
Red	17	visual
Small	13	visual
Round/sphere shaped	8	visual
Stone in centre	8	visual
Grow on trees (cherry trees)	5	other
Has a stork	4	visual
Sweet	3	taste/smell
Pips	3	visual
Black	2	visual
Eaten	2	functional
Associated with trifle	2	other

86) GRAPES

Fruit	20	superordinate
Green	18	visual
Small	16	visual
Used for making wine	14	functional
Black	13	visual
Come in bunches	10	visual
Have seeds	8	visual
Seedless	8	visual
Eaten	8	functional
Grown on vines	7	other
Round	5	visual
Red	3	visual
Stalks	3	visual

87) LEMON

Fruit	20	superordinate
Yellow	19	visual
Citrus	15	other
Bitter taste	10	smell/taste
Sour taste	5	smell/taste
Oval	4	visual
Used in drinks	3	functional
Used to flavour fish	2	functional
Grow on trees	2	other
Slices	2	visual

88) LETTUCE

Salad	18	other
Green	18	visual
Vegetable	16	superordinate
Leaves/leafy	11	visual
Round	3	visual
Mainly water	3	other
Red	2	visual
Crispy	2	tactile
Tasteless	2	taste/smell

Many varieties	2	other
89) MUSHROOMS		
Fungi	15	superordinate
Edible	13	functional
Vegetable	8	superordinate
Short stem/stalk	8	visual
Rounded cap	5	visual
Brown	4	visual
Different types	3	other
Poisonous	3	other
White	2	visual
Grey	2	visual
Grow in dark	2	other
90) ONION		
Vegetable	15	superordinate
Inner/outer layers of skin	15	visual
Strong taste	14	taste/smell
Strong smell	14	taste/smell
Round	14	visual
Can be cooked	13	other
Inner layer greeny-white	8	visual
Can be eaten raw	8	other
Used to flavour dishes	7	functional
Root vegetable	6	superordinate
Makes people cry	6	other
Outer layer brown	3	visual
Spicy	3	taste/smell
Used in salads	3	other
91) ORANGE (19)		
Fruit	19	superordinate
Orange coloured	18	visual
Round/spherical	10	visual
Peel skin to eat	8	associated action
Outer skin	8	visual
Segments in middle	8	visual
Juicy	6	taste/smell
Sweet taste	5	taste/smell
High vitamin C	4	other
Grow on trees	4	other
Citrus	4	superordinate
Grow in hot countries/ climates/tropical	4	other
Used as a drink	2	functional
Imported in Britain	2	other
Pips/seeds	2	visual
Eaten	2	functional
92) PEACH		
Fruit	20	superordinate
Large stone	14	visual
Round	11	visual
Sweet	10	taste/smell
Furry/hairy skin	10	tactile
Peach colour	10	visual
Grow on trees	10	associated action
Soft flesh	9	tactile
Juicy flesh	5	taste/smell

Fleshy	5	visual
Eaten/edible	4	functional
Orange colour	3	visual
Pale colour	2	visual
Similar to a nectarine	2	like a

93) PEANUT

Salted	14	other
Dry-roasted	9	other
Small	8	visual
Allergies/choking	5	other
Can be eaten	3	functional
Natural	3	other
Pub food	3	other
Hard shell	2	tactile
Brown	2	visual
Snack	2	functional

94) PEAR

Fruit	19	superordinate
Green	16	visual
Grow on trees	13	associated action
Bulbous bottom	8	visual
Narrow top	7	visual
Distinct shape	5	visual
Sweet	2	smell/taste
Different types	2	other
Mild taste	2	smell/taste
Juicy	5	smell/taste
Small	2	visual

95) PINEAPPLE

Fruit	20	superordinate
Yellow flesh	9	visual
Leaves on top	7	visual
Spiky	6	tactile
Inedible skin	6	visual
Tropical	5	other
Large	4	visual
Sweet	4	taste/smell
Hard skin	3	tactile
Hot countries	3	other
Soft centre	2	tactile
Grow on trees	2	other

96) POTATO

Root vegetable	13	superordinate
Ground grown	10	other
Vegetable	7	superordinate
Boiled	6	other
Mashed	6	other
Roasted	4	other
Chipped	4	other
Brown	4	visual
Starch	3	other
Baked	2	other
Carbohydrate	2	other
Round	2	visual

97) PUMPKIN

Halloween	18	other
Orange	17	visual
Large	15	visual
Vegetable	10	superordinate
Fruit	8	superordinate
Insides scraped out and face made	8	other
Sphere/ball/round shaped	6	visual
Edible	5	functional
Lots of seeds	4	visual
Lanterns/candles put in them	4	functional
Inside used for pies	4	functional
Inside used for soups	2	functional

98) STRAWBERRY

Fruit	20	superordinate
Red	20	visual
Seeds out	10	visual
Summer	8	other
Small	7	visual
Sweet	5	taste/smell
Ground grown	5	other
Eat with cream	5	other
Soft	4	tactile
Pick your own	3	other
Lots seeds	2	visual
Green stem	2	visual
Juicy	2	taste/smell
Heart shaped	2	visual

99) TOMATO

Red	20	visual
Fruit	15	superordinate
Seeds	9	visual
Edible	8	functional
Salad	6	other
Vegetable	5	superordinate
Round	5	visual
Raw/cooked	3	other
Fruit or vegetable?	2	other
Juicy	2	taste/smell
Flesh	2	visual
Soft	2	tactile
Ripe	2	taste/smell

100) WATERMELON

Fruit	18	superordinate
Lots of seeds	11	visual
Green outside	10	visual
Large	10	visual
Red	8	visual
Watery/succulent	7	taste/smell
Round	7	visual
Juicy	5	tactile
Fleshy	3	tactile
Grow abroad/exotic countries	3	other
Type of melon	2	superordinate
Pink	2	visual
Eaten as starter	2	functional
Eaten as dessert	2	functional

Striped shell	2	visual
Hard outside	2	tactile

FURNITURE (12)

101) ASHTRAY		
Flick ash	13	associated action
Like a dish/bowl	12	like a
Put out cigarette	9	associated action
Object/item	9	superordinate
Ash placed/collected in	6	functional
Small	4	visual
Metal/glass	3	visual
Container	3	superordinate
Used by smokers	2	other

102) BED		
Used to sleep in /on	20	functional
Piece/item of furniture	14	superordinate
Duvet	8	visual
Made of wood	8	visual
Pillows	7	visual
Blankets	5	visual
Found in the bedroom	4	other
Warm	3	tactile
Mattress on top	3	visual
Four-poster	2	other

103) CHAIR		
Sit on it	19	functional
4 legs	13	visual
Back	12	visual
Seat	5	visual
Wooden	3	visual
Plastic	3	visual
Different types	3	other
Different materials	2	visual
Comfy	2	other

104) DESK		
Used to work on	16	functional
Piece/item of furniture	15	superordinate
Similar to a table	11	like a
Four-legged	9	visual
Table	9	other
Wooden	7	visual
Used for writing on	7	functional
Has drawers	6	visual
Designed related to work type	4	other
Flat top	4	visual
Level base	3	visual
Legs used for support	3	visual
Shelves	2	visual

105) DRESSER		
Furniture	15	superordinate
Kitchen/dining room	8	other
Drawer	8	visual
Mirrored	6	visual
Bedroom	6	other

Wooden	6	visual
Storage unit	4	functional
Display things	3	functional
Accommodate plates	3	functional
Hold belongings	2	functional
Like a cabinet	2	like a
Large	2	visual
On 4 legs	2	visual
Crockery	2	other
106) LAMP		
Light	16	visual
Electrical	7	other
Glass bulb	6	visual
Illuminates small areas	5	functional
Lights room	5	functional
On table	4	visual
Small	3	visual
Object	3	superordinate
Household	3	other
Indoor/outdoor	2	other
Base	2	visual
107) RECORD PLAYER		
Plays records	17	functional
Equipment	8	superordinate
Needle	8	visual
Sound	6	auditory
Grooves	3	visual
Amplifier	3	other
Stylus	3	visual
Disks	2	visual
Machine	2	superordinate
Old fashioned	2	other
Electrical	2	other
Vinyl	2	visual
Rotates/spins	2	associated action
Part of soundsystem	2	superordinate
108) ROCKING CHAIR		
Rockers on bottom	14	visual
It rocks	11	associated action
Seat	8	visual
Chair	8	superordinate
Sit/sat on	4	functional
Wooden	4	visual
Piece of furniture	3	superordinate
Elderly people	2	other
Mothers	2	other
109) SOFA		
Piece/item of furniture	17	superordinate
Used to sit on/sat upon	16	functional
Seat one/two/three/four people/variety of sizes	11	visual
Cushions	8	visual
Long	4	visual
Wooden frame	4	visual
Soft	3	tactile
Comfortable	3	other

Hard frame	2	tactile
People relax on it	2	associated action
Two arms	2	visual
Variety of shapes	2	visual
Variety of colours	2	visual

110) TABLE

Four-legged	16	visual
Flat surface	16	visual
Piece/item of furniture	11	superordinate
Used for eating off/on	11	functional
Made of wood	10	visual
Found in the kitchen	10	other
Rectangular	8	visual
Found in dining room	7	other
Round	7	visual
Work on surface	6	functional
Plastic	4	visual
Object	4	superordinate
Various styles	4	visual
Many legs	3	visual
Many purposes	3	other
Go with chairs	2	other

111) TELEVISION

Produces images	12	associated action
Produces sound	9	associated action
Entertainment	8	functional
Electrical	8	other
Media	5	other
Transmission	5	other
Square	5	visual
Box	4	visual
20th century	3	other
Object	2	superordinate
Equipment	2	superordinate
Different sizes	2	visual
Colour or black & white	3	other

112) VASE

Display flowers	20	functional
Pottery/glass	9	visual
Hold water	9	functional
Long/tall	6	visual
Object	5	superordinate
Decorative	3	other
Receptacle	2	superordinate

INSECTS (8)

113) ANT

Insect	18	superordinate
Small	18	visual
Colonial	7	other
Red/black	6	visual
Very strong	5	other
Very social	5	other
6 legs	3	visual
Can bite	2	associated action
Hardworking	2	other

Summer	2	other
114) BEE		
Insect	19	superordinate
Yellow/black	13	visual
Stings	11	associated action
Honey	11	taste/smell
Flies	7	associated action
Stripy	7	visual
Buzzes	7	auditory
Small	6	visual
Wings	4	visual
Eat pollen	5	associated action
Lives in hive	5	other
Colony	2	other
115) BEETLE		
Insect	17	superordinate
Black	14	visual
Small	13	visual
Hard shell	9	tactile
Six legs	6	visual
Shell for protection	5	visual
Wings	2	visual
Shiny	2	visual
Eight legs	2	visual
Can fly	2	associated action
116) BUTTERFLY		
Insect	16	superordinate
Pair of wings (coloured)	16	visual
Produced from caterpillar	8	other
Beautiful	8	visual
Many colours	6	visual
Flies	4	associated action
Mirror-image/symmetrical wings	3	visual
Small/little	3	visual
Many species/types	2	other
Seen in summer	2	other
Collectible	2	other
Collect pollen	2	other
Small/thin body	2	visual
117) CATERPILLAR		
Butterfly/moth	14	other
Insect	12	superordinate
Long	10	visual
Eats leaves	7	other
Lots of legs	4	visual
Small	3	visual
Thin	3	visual
Furry	2	tactile
Green	2	visual
Live in garden	2	other
118) FLY		
Insect	18	superordinate
Small	13	visual
Flies	9	associated action

Wings	8	visual
Buzzes	6	auditory
Black	6	visual
Unhygienic	5	other
6 legs	3	visual
Common	2	other

119) GRASSHOPPER

Insect	18	superordinate
Jumps	12	associated action
Green/brown	12	visual
Noise	8	auditory
Small	7	visual
Rubs legs	3	associated action
Long legs	3	visual

120) SPIDER

8 legs	18	visual
Spins webs	10	associated action
Scary	9	other
Small	4	visual
Insect	4	superordinate
Web used to catch flies	4	other
Creature	3	superordinate
Crawls/scuttles	3	associated action
Black	3	visual
Body	3	visual
Eats insects/flies	3	associated action
Arthropod	2	superordinate
Arachnid	2	superordinate
Deadly/not	2	other
Creepy	2	other

KITCHEN ITEMS (18)

121) BOTTLE

Hold liquid	18	visual
Glass	14	visual
Container	10	superordinate
Plastic	7	visual
Tall	2	visual
Resealable	2	other
Pouring	2	associated action
Alcohol	2	other

122) BROOM

Sweeping	17	associated action
Long	9	visual
Bristles	9	visual
Wood	7	visual
Stick	7	visual
Item	5	superordinate
Handle	5	visual
Instrument/item	5	superordinate
Cleaning	4	functional
Like a brush	3	like a
Tool	2	superordinate
Object	2	superordinate
Witches	2	other

123) BOWL

Store/hold food	12	functional
Eat food out	4	functional
Plastic	4	visual
Glass/pot	3	visual
Container	3	superordinate
Steep sides	3	visual
Crockery	3	superordinate
Object	2	superordinate
Cooking utensil	2	superordinate
Round	2	visual

124) CLOCK

Tells time	17	functional
2 hands	10	visual
Device	9	superordinate
Circular	5	visual
Numbers	5	visual
Face	4	visual
Hour hand	2	visual
Minute hand	2	visual
Hands move around face	2	associated action

125) CUP

Drink out of	17	functional
Has handle	10	visual
Contains/holds liquid	7	functional
Saucer	4	other
Ceramic	4	visual
Container	3	superordinate
Tea	2	other
Large or small	2	visual
Vessel	2	superordinate
Small	2	visual
Hot drink	2	other

126) FORK

Piece of cutlery	12	superordinate
Prongs (three or four)	12	visual
Handle	12	visual
Handle used to pick up food	11	functional
Used for eating	11	functional
Implement	7	superordinate
Stab food	4	associated action
Utensil	3	superordinate
Sharp points	3	tactile
Found in the kitchen	3	other
Knife	2	other

127) FRYING PAN

Used to fry/cook food	19	functional
Kitchen utensil	7	superordinate
Handle	6	visual
Object	6	superordinate
Round	5	visual
Shallow	5	visual
Flat	5	visual
Metallic	4	visual
Place on hob	3	associated action
Heat cooks the food	3	other

Used to cook eggs	3	functional
Non-stick	2	other
Large	2	visual
Oil heated	2	other

128) JUG

Used to hold liquid	18	functional
Container	12	superordinate
Pouring	12	associated action
Handle on side	12	visual
Kitchen item/utensil/implement	8	superordinate
Made of china	8	other
Made of glass	8	other
Made of plastic	6	other
Lip for pouring out of	6	functional
Round	5	visual
Various sizes	4	visual
Different shapes	3	visual
Vessel	3	superordinate
Used to measure liquid	3	functional
Measurements up the side	3	visual

129) KETTLE

Used to boil water	20	functional
Has a spout	12	visual
Electric/electrical	11	other
Kitchen item	9	superordinate
Made of metal	9	visual
Spout used to pour water	9	functional
For making tea	8	functional
Container	8	superordinate
Made of plastic	8	visual
Has lid	7	visual
For making coffee	6	functional
Has a handle	6	visual
Put on stove	5	associated action
Whistles when boiled	5	associated action
Different styles	4	visual
Variety of shapes	3	visual
Object	2	superordinate
Element	2	other

130) KNIFE

Cut things	16	functional
Sharp	15	tactile
Instrument	11	superordinate
Blade	10	visual
Metal	10	visual
Handle	7	visual
Eat with it	5	functional
Weapon	4	superordinate
Use with fork	3	other
Serrated teeth	2	tactile

131) REFRIGERATOR

Keeps food cold	20	functional
Stops deterioration/preserves food	8	functional
Powered by electricity	8	other
Found in kitchen	7	other

Appliance	5	superordinate
White	3	visual
Holds food/drink	2	functional
Container	2	superordinate

132) ROLLING PIN

Flatten pastry	19	functional
Wooden	13	visual
Cylindrical/round	11	visual
Kitchen utensil	8	superordinate
Long	7	visual
Object	4	superordinate
Baking	3	other
Solid	2	tactile

133) SALTCELLAR

Stores salt	12	functional
Sprinkled on food	10	associated action
Container	9	superordinate
Holes on top	8	visual
Dispenser	5	superordinate
On tables	2	other

134) SAUCEPAN

Used for cooking	16	functional
Made of metal	13	visual
Things heated up within	12	functional
Put on stove/oven/hob/flame	12	associated action
Kitchen item/utensil	10	superordinate
Implement	9	superordinate
Has a handle	9	visual
Round	7	visual
Container	5	functional
Lip for pouring	5	visual
Heat resistant/proof	5	other
Lid	4	visual
Many sizes	4	visual
Different styles	4	visual
Deep	3	visual
Bowl	2	visual
Plastic handle	2	visual

135) SPOON

Eat with it	15	functional
Round end	9	visual
Kitchen utensil	8	superordinate
Handle	7	visual
Cutlery	7	superordinate
Scoop things	5	functional
Object	4	superordinate
Metal	4	visual
Plastic	2	visual
Use for cooking	2	associated action
Stainless steel	2	visual
Eat soup	2	associated action

136) STOVE

Cooker	16	like a
Heat/cook food	14	functional
Gas	6	other

Old fashioned	3	other
Electric	5	other
Kitchen	4	other
Gets hot	2	other
137) TOASTER		
Toast	15	functional
Instrument	15	superordinate
Electrical	10	other
Cook bread	9	functional
Kitchen	6	other
Machine	4	superordinate
Crispy	3	tactile
2 slots	2	visual
Heated	2	other
138) WINEGLASS		
Glass	14	superordinate
Holds wine	13	functional
Stem	11	visual
Used to drink from	6	functional
Small	3	visual
Rounded	3	visual
Container	2	superordinate
Fragile	2	tactile
Utensil	2	superordinate

MUSICAL INSTRUMENTS (10)

139) ACCORDION		
Musical instrument	19	superordinate
Contains air	7	other
Squeeze	6	associated action
Keyboard	5	visual
Lots of buttons	5	visual
Bellows	2	other
Like a small piano	2	like a
Sailors	2	other
Noisy	2	auditory
140) BELL		
Metal	13	visual
Rings	12	auditory
Church	6	other
Cone shape	6	visual
Sound	4	auditory
Ball inside	4	visual
Object	4	superordinate
Instrument	3	superordinate
Clanging sound	3	auditory
Handle	2	visual
Shake it	2	associated action
141) DRUM		
Bang it/hit it with stick/hand/ brush	19	associated action
Musical instrument	14	superordinate
Material/skin stretched over top	12	visual
Makes loud banging noise	10	auditory
Round shape	6	visual

Used to produce sound	5	functional
Used to keep rhythm/beat	5	functional
Cylindrical	4	visual
Percussion	2	superordinate
Large or small	2	visual

142) FLUTE

Instrument	20	superordinate
Long	9	visual
Play sideways	8	other
Silver	7	visual
Pipe-like	6	like a
Blow through nose	6	other
Valves/keys	5	visual
Hi-pitched	4	auditory
Different sounds	4	auditory
Wind	4	other
Mouthpiece	3	visual
Use fingers	2	other
Wood	2	visual

143) FRENCH HORN

Musical instrument	20	superordinate
Brass	13	visual
Blow it	7	other
Wind	4	other
Orchestra	4	other
Use fingers to press keys	4	other
Large	2	visual

144) GUITAR

Musical instrument	20	superordinate
Stringed	19	visual
Main body of instrument	11	visual
Makes music	10	functional
Play it	10	other
Electric	10	other
Acoustic	9	other
Made of wood	9	visual
Six strings	8	visual
Stem	8	visual
Strings are plucked	7	associated action
Strumming	6	associated action
Many shapes	5	visual
Many sizes	4	visual
12 strings	4	visual
Played with hands	4	other
Pegs	3	visual
Solo	2	other
Different notes	2	auditory
Made of metal	2	visual

145) HARP

Stringed	15	visual
Plucked	10	associated action
Instrument (musical)	5	superordinate
Large	4	visual
Angels/heaven association	3	other
Wooden frame	2	visual

146) PIANO

Musical instrument	20	superordinate
Stringed	12	visual
Keys	10	visual
Used to make/create music	8	functional
Made of wood	7	visual
Black and white keys	6	visual
Hammers bang on the strings	5	other
Large	4	visual
Heavy	3	tactile
Keys pressed to vibrate strings	5	other
Sit at the instrument	2	other
Ebony and ivory	2	visual
Pedals	2	visual

147) TRUMPET

Instrument	19	superordinate
Brass	19	visual
Valves	3	visual
Orchestra	3	other
Use air	3	other
Blown into	2	other
Metal	2	visual
Valves/buttons/keys pressed	2	other
Wind instrument	2	superordinate
Small	2	visual

148) VIOLIN

Musical instrument	18	superordinate
Bow	15	visual
Stringed	13	visual
Play it	6	associated action
Under chin	6	other
Small	5	visual
Wooden	5	visual
4 strings	5	visual
Make sound	5	auditory
Orchestra	2	other
Pluck it	2	other
Like a guitar	2	like a

TOOLS (13)

149) AXE

Cutting/chopping wood	18	functional
Wooden handle	11	visual
Metal cutting blade/edge	9	visual
Tool/implement	8	superordinate
Large blade	2	visual
Sharp edge	2	tactile
Weapon	2	superordinate
Long handle	2	visual

150) CHISEL

Tool	16	superordinate
Woodworking	12	functional
Metal	9	visual
Chipping	7	functional
Thin	5	visual
Used with hammer	4	other

Handle	4	visual
Sculpture	3	functional
Plaster off walls	3	other
Sharp tip/edge	2	tactile
Flat head	2	visual
Used on stone	2	other
151) HAMMER		
Tool	20	superordinate
Handle	19	visual
Used for knocking in things/ nails	17	functional
Metal head	15	visual
Handle made of wood	14	visual
Nails knocked/banged into walls/wood	10	associated action
Hammer swung	3	associated action
DIY	2	other
Steel end	2	visual
Heavy top part	2	tactile
152) LADDER		
Used to climb things	11	functional
Used to reach heights/high places	11	functional
Rungs	11	visual
Long	4	visual
Poles	4	visual
Wooden	4	visual
Steps	3	visual
Two rails/sides	3	visual
Object	3	superordinate
Piece of apparatus/equipment	2	superordinate
Metal	2	visual
Associated with window cleaning	2	other
Rested/leaned upon a wall	2	other
Tool	2	superordinate
153) PAINTBRUSH		
Used to paint with	16	functional
Has bristles/hair	14	visual
Pictures painted with it/used to create art	11	functional
Used for decorating	4	functional
Has a handle	4	visual
Dabbed in paint	3	associated action
Different sizes	2	visual
Wooden handle	2	visual
Stick like	2	like a
Tool/implement	4	superordinate
Fine end	2	visual
154) PENCIL		
Writing implement	17	functional
Wooden surrounding/exterior	12	visual
Lead	10	visual
Graphite	9	visual
Used for drawing/sketching	8	functional
Leaves marks/impressions on	7	other

paper		
Thin	5	visual
Long	3	visual
Carbon	3	visual
Used with rubbers/rubbed out	3	other
Light/dark grey	2	visual
Graphite hardness/softness	2	tactile
Has a tip	2	visual
155) PLIERS		
Tool	8	superordinate
Metal	8	visual
Used to pull things out/apart	8	functional
Instrument	4	superordinate
Used for cutting wire	4	functional
Used to grip/clamp	4	functional
Two handles	3	visual
Object	3	superordinate
Like scissors	3	like a
Like tweezers	2	like a
Handles are squeezed	2	associated action
Hand-held	2	other
Pincers	2	visual
156) RULER		
Measure	14	functional
Draw straight line	10	associated action
Distance/length	8	other
Instrument	8	superordinate
Straight	6	visual
Wood	6	visual
Plastic	5	visual
cm/mm	3	other
Long	2	visual
Numbers	2	visual
157) SAW		
Cut wood	13	associated action
Serrated/jagged edge	10	visual
Sharp	8	tactile
Tool	6	superordinate
Handle	6	visual
Metal	6	visual
Cutting things	5	associated action
Utensil	5	superordinate
Object	4	superordinate
Blade	4	visual
Teeth	4	visual
Carpenter	3	other
158) SCISSORS		
Used for cutting paper/card	20	functional
Used for cutting things	15	functional
Two blades	12	visual
Sharp	8	tactile
Made of metal	7	visual
Used for cutting fabric/material	7	functional
Implement/tool	6	superordinate
Blades pushed/work together	6	associated action
Attached/joined/interlocking	5	visual

Two handles	4	visual
Used for cutting hair	3	functional
Controlled by thumb and forefinger	3	other
Two holes at end	3	visual
Two holes for thumb and forefinger	3	functional
Instrument	2	superordinate
Plastic handle	2	visual
159) SCREW		
Metal	12	visual
Hold things together	12	functional
Wood	5	visual
Thread	4	visual
Various size/shapes	4	visual
Long/thin	4	visual
Screwdrivers	3	other
Cylindrical	3	visual
Fixing things	2	other
Object	2	superordinate
Head	2	visual
Grooves/ridges	2	visual
160) SCREWDRIVER		
Tool	19	superordinate
Used to tighten/loosen screws	18	functional
Used for screwing	10	functional
Screw into wood/metal/ masonry/plastic	10	other
Various types	8	other
Plastic handle	7	visual
Long	7	visual
Metal pole	7	visual
Manual	6	other
Electric	5	other
Various sizes	5	visual
Rotated in the hand	4	other
Phillips	2	other
Crosshead	2	other
Thin	2	visual
Tip of pole changes shape	2	other
161) SPANNER		
Tool	19	superordinate
Used to tighten/loosen nuts/ bolts	17	functional
Made of metal	12	visual
Many sizes	11	visual
Manual	8	other
Used to fit together beds/tables cars	8	functional
Used by mechanics	5	other
Need to match end to nut size	3	other
DIY	3	other
Used by engineers	2	other

VEHICLES (12)

162) AEROPLANE		
Flies	18	associated action
Vehicle	8	superordinate
Large	6	visual
Carries passengers	7	functional
Transport	9	functional
Wings	9	visual
Very fast	5	other
Long distance	3	other
Engine power	6	other
Machine	2	superordinate
Carries freight/cargo	3	functional
163) BICYCLE		
Two wheels	20	visual
Transport system	9	functional
Vehicle	8	superordinate
Pedal to move	8	associated action
Person/human/leg powered	6	other
Has pedals	5	visual
Has handlebars	5	visual
Has seat	5	visual
Ride/sit on	4	associated action
Used on own	4	other
Has frame	4	visual
Has gears	2	visual
No engine	2	other
Steers	2	associated action
164) BUS		
Vehicle	16	superordinate
Used to transport people	16	functional
Lots of seats	10	visual
Moves along	9	associated action
Large	7	visual
Passengers	5	other
Long	5	visual
Driver	5	other
Public transport	4	other
Four-wheels	3	visual
Traditional London bus	2	other
Red	2	visual
165) CAR		
Used to transport people	19	functional
Motor vehicle	18	superordinate
Four wheels	18	visual
Engine powered	13	other
Has two/three/four/five seats	13	visual
Petrol cars	8	other
Four tyres	6	visual
Diesel cars	4	other
Are driven	4	associated action
Metal body/bodywork	3	visual
Electric cars	2	other
Fast	2	other
Popular	2	other
Private	2	other
Steering wheel	2	visual
Has a radio	2	visual

Different models	2	visual
166) HELICOPTER		
Rotating blades/propellers	12	associated action
Flying vehicle/aircraft machine	9	superordinate
It flies	7	associated action
Mode of transport	5	superordinate
Propellers	4	visual
Hovers	4	associated action
Small rotor on tail	3	visual
Used for rescuing/emergency vehicle	3	functional
Smaller than aeroplane	2	visual
Transports people	2	functional
For the rich	2	other
Used for flying	2	functional
Large rotor on top	2	visual
Tail	2	visual
Engine keeps in air	2	other
167) MOTORCYCLE		
Two-wheeled	18	visual
Engine/motor powered	17	other
Vehicle	7	superordinate
Used as transport	6	functional
Petrol powered	5	other
Carries one or two people	5	functional
Fast	3	other
Many sizes/types	3	visual
Handlebars	3	visual
Seat	2	visual
Dangerous	2	other
Used in sport	2	functional
Bicycle	2	like a
You ride it	2	associated action
168) ROLLERSKATE		
4 wheels	20	visual
Boot	15	visual
Shoe	5	superordinate
Travel	5	other
Leisure	3	other
Roll on floor	2	associated action
Foot	2	other
Pair	2	other
169) SAILBOAT		
Wind power	12	other
Floats	8	associated action
Sails	7	associated action
Vessel	6	superordinate
Transport	6	functional
Waterfaring	4	associated action
Boat	3	like a
Leisure	3	other
Miniature/small	3	visual
Lakes/rivers	2	other
Sit in it	2	other
170) SLEDGE		

Used in snow/wintry weather	12	functional
Move/glide along snow/frozen materials	9	associated action
Used to slide down hills	8	functional
Two runners/rails on underside	7	visual
Runners used for movement	6	functional
Used for fun	6	functional
Dogs (huskies) pull them in cold weather	4	other
Transport/used to carry people	5	functional
Seat (wooden)	4	visual
Smooth undersurface	3	tactile
Seat (plastic)	3	visual
Used mainly by children	3	other
Vehicle	3	superordinate

171) TRAIN

Transport	18	functional
Rail track	15	other
Carriages	8	visual
Large no. passengers	6	other
Carry freight	6	functional
Different powers	3	other
Long	3	visual
Seats	3	visual
Vehicle	2	superordinate
Steam	2	other
Electric	2	other
Engine	2	other
Speed	2	associated action

172) TRUCK

Vehicle	17	superordinate
Transport	12	functional
Large	11	visual
Driven	5	other
Wheels	4	visual
Small lorry	3	other

173) WAGON

Transport	16	functional
Pulled along	12	other
Wheels	8	visual
Horses	6	visual
America	5	other
Vehicle	4	superordinate
Wild west	4	other
Cart	3	like a
Wooden	2	visual
Carry goods	2	associated action
18th century	2	other
Large	2	visual

APPENDIX B
GLOSSARY OF BRAIN AREA ACRONYMS

L	Left
R	Right
B	Bilateral
FFG	Fusiform gyrus
LG	Lingual gyrus
IFG	Inferior frontal gyrus
ITG	Inferior temporal gyrus
MTG	Middle temporal gyrus
PM	Premotor area
IMTG	Inferior middle temporal gyrus
PMTG	Posterior middle temporal gyrus
PTG	Posterior temporal gyrus
TOJ	Temporo-occipital junction
IPG	Inferior parietal gyrus
AMTG	Antero-medial temporal gyrus
MFG	Middle frontal gyrus
PHG	Parahippocampal gyrus
SMG	Supramarginal gyrus
STG	Superior temporal gyrus
T	Thalamus
ATG	Anterior temporal gyrus
IOG	Inferior occipital gyrus
DLPFG	Dorso-lateral prefrontal gyrus
SPG	Superior parietal gyrus
PC	Precuneus
C	Cuneus
CB	Cerebellum
MOG	Medial occipital gyrus
LFFG	Lateral fusiform gyrus
MFFG	Medial fusiform gyrus
MPTG	Middle posterior temporal gyrus
AFFG	Anterior fusiform gyrus
EXS	Extrastriate
PCG	Precentral gyrus
ITO	Inferior temporo-occipital
OT	Occipito-temporal
CP	Centro-parietal
FC	Fronto-central
SLXN	Sub-lobar extranuclear
CBAL	Cerebellum anterior lobe
TSBG	Temporal subgyral
SLI	Sub-lobar insula
IC	Interhemispheric cuneus
TSMG	Temporal supramarginal gyrus
PC	Precuneus
OSBG	Occipital subgyral
I	Insula
POCG	Postcentral gyrus
U	Uncus

CPD	Cerebellum posterior declive
PSBG	Parietal sub-gyral
PSMG	Parietal supramarginal gyrus
OMTG	Occipital middle temporal gyrus
AC	Anterior cingulated
PCT	Posterior cerebellar tonsil
CG	Cingulate gyrus
CTB	Cerebellar tuber
FSBG	Frontal subgyral

APPENDIX C

SnPM group analysis for MEG experiment 1. Naming overtly.

Condition	Timing (sec)	Trigger	Frequency (Hz)	t-value	p-level	T/C			Power	Cortical area of activity	BA
L v NL	0.3 v 0.3	1 v 2	5-15		Not sig						
L v NL	0.3 v 0.3	1 v 2	10-20		Not sig						
L v NL	0.3 v 0.3	1 v 2	15-25		Not sig						
L v NL	0.3 v 0.3	1 v 2	20-30		Not sig						
L v NL	0.3 v 0.3	1 v 2	25-35		Not sig						
L v NL	0.3 v 0.3	1 v 2	30-40		Not sig						
L v NL	0.7 v 0.7	1 v 2	5-15		Not sig						
L v NL	0.7 v 0.7	1 v 2	10-20		Not sig						
L v NL	0.7 v 0.7	1 v 2	15-25	4.85	0.031	27	-15	-15	ERS	Right limbic parahippocampal gyrus	
L v NL	0.7 v 0.7	1 v 2	20-30		Not sig						
L v NL	0.7 v 0.7	1 v 2	25-35		Not sig						
L v NL	0.7 v 0.7	1 v 2	30-40		Not sig						
L v baseline	0.3 v –0.5	1 v 1	5-15	5.95	0.023	-24	3	-9	ERD	Left sub-lobal, extranuclear	
L v baseline	0.3 v –0.5	1 v 1	10-20	6.86	0.016	42	-66	18	ERD	Right middle temporal gyrus	
				6.05	0.031	-33	-39	-30	ERD	Left cerebellum, anterior lobe	
				5.74	0.047	39	-48	0	ERD	Right temporal lobe, sub-gyral	
L v baseline	0.3 v –0.5	1 v 1	15-25	10.33	0.004	42	-15	12	ERD	Right sub-lobar insula	13
				9.09	*0.004*	*0*	*-75*	*36*	*ERD*	Interhemispheric cuneus	
				7.74	*0.004*	*51*	*-51*	*24*	*ERD*	*Right temporal, supramarginal gyrus*	
				7.21	0.004	-60	-24	15	ERD	Left parietal postcentral gyrus	40
				6.46	*0.016*	*-63*	*-36*	*-3*	*ERD*	*Left middle temporal gyrus*	*21*
				6.32	*0.020*	*-54*	*-15*	*39*	*ERD*	*Left parietal postcentral gyrus*	*3*
				6.70	0.008	18	54	33	ERD	Right superior frontal gyrus	9
				6.56	0.012	-42	-51	39	ERD	Left inferior parietal lobule	
				5.59	*0.043*	*-33*	*-66*	*42*	*ERD*	*Left parietal precuneus*	*19*
				6.16	0.031	42	-48	63	ERD	Right parietal postcentral gyrus	5
				5.78	0.035	-33	-54	60	ERD	Left superior parietal lobule	7
L v baseline	0.3 v –0.5	1 v 1	20-30	7.00	0.016	45	-30	-12	ERD	Right temporal lobe sub-gyral	

				6.09	0.023	18	-78	39	ERD	Right parietal precuneus	
L v baseline	0.3 v –0.5	1 v 1	25-35	7.13	0.008	-60	9	-6	ERD	Left superior temporal gyrus	22
				7.00	0.008	27	45	24	ERD	Right superior frontal gyrus	
				6.85	0.008	-42	-60	12	ERD	Left middle temporal gyrus	
				6.21	*0.023*	*-42*	*-39*	*15*	*ERD*	*Left superior temporal gyrus*	
				6.46	0.012	-18	-51	63	ERD	Left parietal postcentral gyrus	7
				6.39	0.016	-57	21	36	ERD	Left middle frontal gyrus	
				6.14	0.031	24	63	-6	ERD	Right superior frontal gyrus	10
				6.00	0.039	24	-51	69	ERD	Right parietal postcentral gyrus	9
				5.85	0.047	30	-27	-15	ERD	Right limbic parahippocampal gyrus	
L v baseline	0.3 v –0.5	1 v 1	30-40		Not sig						
NL v baseline	0.3 v –0.5	2 v 1	5-15		Not sig						
NL v baseline	0.3 v –0.5	2 v 1	10-20		Not sig						
NL v baseline	0.3 v –0.5	2 v 1	15-25	7.98	0.008	-24	-72	27	ERD	Left occipital sub-gyral	
				7.92	*0.008*	*3*	*-75*	*36*	*ERD*	*Right occipital lobe cuneus*	
				7.92	*0.008*	*-21*	*-60*	*33*	*ERD*	*Left parietal precuneus*	
				6.86	0.012	-51	-6	24	ERD	Left frontal precentral gyrus	
				6.38	*0.027*	*-42*	*-21*	*6*	*ERD*	*Left superior temporal gyrus*	*13*
				6.28	0.027	66	-33	9	ERD	Right superior temporal gyrus	22
				6.11	0.027	45	-18	18	ERD	Right sub-lobar insula	
				5.99	*0.031*	*51*	*-6*	*24*	*ERD*	*Right frontal precentral gyrus*	
NL v baseline	0.3 v –0.5	2 v 1	20-30	7.85	0.004	30	-18	-24	ERD	Right limbic parahippocampal gyrus	
				7.41	*0.004*	*51*	*-30*	*-18*	*ERD*	*Right inferior temporal gyrus*	
				6.86	0.004	45	-24	54	ERD	Right parietal postcentral gyrus	
				6.22	0.016	-3	-75	36	ERD	Left occipital cuneus	
				5.91	0.020	33	48	33	ERD	Right superior frontal gyrus	9
NL v baseline	0.3 v –0.5	2 v 1	25-35	9.71	0.004	-15	-42	21	ERD	Left sub-lobar extra nuclear	
				8.69	*0.004*	*-12*	*-54*	*54*	*ERD*	*Left parietal precuneus*	
				6.99	*0.020*	*-33*	*-57*	*60*	*ERD*	*Left superior parietal lobule*	7
				7.54	0.008	36	-15	-30	ERD	Right limbic lobe uncus	20
				7.20	*0.012*	*39*	*-12*	*-39*	*ERD*	*Right inferior temporal gyrus*	*20*
				6.72	0.020	60	6	39	ERD	Right middle frontal gyrus	
				6.49	*0.020*	*42*	*-45*	*15*	*ERD*	*Right superior temporal gyrus*	
				6.27	*0.020*	*48*	*-27*	*24*	*ERD*	*Right inferior parietal lobule*	

				6.11	0.027	6	45	27	ERD	Right medial frontal gyrus	
				6.03	0.035	30	-54	48	ERD	Right superior parietal lobule	7
				5.73	*0.047*	*21*	*-51*	*45*	*ERD*	*Right parietal precuneus*	*7*
				5.58	*0.047*	*21*	*-66*	*42*	*ERD*	*Right parietal precuneus*	
				5.74	0.047	-33	-75	-21	ERD	Left cerebellum posterior declive	
NL v baseline	0.3 v –0.5	2 v 1	30-40		Not sig						
L v baseline	0.7 v –0.5	1 v 1	5-15	8.54	0.008	39	63	6	ERS	Right middle frontal gyrus	10
				7.60	*0.008*	*3*	*69*	*-6*	*ERS*	*Right middle frontal gyrus*	
				7.10	*0.012*	*-39*	*48*	*-6*	*ERS*	*Left middle frontal gyrus*	
				6.76	0.012	33	-81	15	ERD	Right middle occipital gyrus	
				5.51	0.039	-9	-99	21	ERD	Left occipital cuneus	18
L v baseline	0.7 v –0.5	1 v 1	10-20	6.72	0.031	-9	66	-9	ERS	Left superior frontal gyrus	10
				6.12	*0.031*	*-3*	*66*	*9*	*ERS*	*Left frontal lobe*	
				8.43	0.016	-42	-72	-6	ERD	Left inferior occipital gyrus	19
				6.50	0.031	51	-60	0	ERD	Right middle temporal gyrus	37
				6.34	*0.031*	*36*	*-78*	*15*	*ERD*	*Right middle occipital gyrus*	
				6.65	0.031	6	-66	45	ERD	Right parietal precuneus	
				6.21	0.031	-63	-33	24	ERD	Left inferior parietal lobule	40
				5.89	0.047	-21	-51	39	ERD	Left parietal sub-gyral	
				5.88	*0.047*	*-21*	*-60*	*45*	*ERD*	*Left superior parietal lobule*	*7*
L v baseline	0.7 v –0.5	1 v 1	15-25	8.05	0.008	-9	-48	39	ERD	Left parietal precuneus	7
				7.65	0.008	-57	-21	24	ERD	Left parietal postcentral gyrus	
				6.67	0.020	-27	-78	-9	ERD	Left middle occipital gyrus	
				6.23	*0.023*	*-12*	*-69*	*-18*	*ERD*	*Left cerebellum posterior declive*	
				6.48	0.020	30	-60	51	ERD	Right superior parietal lobule	7
L v baseline	0.7 v –0.5	1 v 1	20-30	6.00	0.020	-57	-45	30	ERD	Left parietal supramarginal gyrus	
				5.96	0.020	24	-78	27	ERD	Right occipital precuneus	
				5.71	0.023	-36	-51	51	ERD	Left inferior parietal lobe	40
				5.64	0.023	36	-15	-12	ERD	Right temporal lobe sub-gyral	
				5.54	*0.027*	*39*	*-21*	*-6*	*ERD*	*Right temporal lobe sub-gyral*	
L v baseline	0.7 v –0.5	1 v 1	25-35		Not sig						
L v baseline	0.7 v –0.5	1 v 1	30-40		Not sig						
NL v baseline	0.7 v –0.5	2 v 1	5-15	7.04	0.016	-12	69	-6	ERS	Left medial frontal gyrus	
				6.20	*0.027*	*-33*	*63*	*12*	*ERS*	*Left middle frontal gyrus*	*10*

				6.88	0.020	24	-81	9	ERD	Right occipital cuneus	
				6.75	*0.020*	*45*	*-95*	*12*	*ERD*	*Right middle temporal gyrus*	*39*
				6.34	0.020	-36	-63	-3	ERD	Left temporal lobe sub-gyral	
				6.13	0.031	-9	-87	-3	ERD	Left occipital lingual gyrus	
NL v baseline	0.7 v –0.5	2 v 1	10-20	9.71	0.004	39	-69	12	ERD	Right temporal lobe sub-gyral	
				8.51	*0.004*	*48*	*-57*	*-6*	*ERD*	*Right middle occipital gyrus*	
				7.88	0.008	12	-63	51	ERD	Right parietal precuneus	
				6.44	*0.023*	*27*	*-60*	*51*	*ERD*	*Right superior parietal lobule*	*7*
				7.74	0.008	-27	-75	-12	ERD	Left occipital lobe fusiform gyrus	19
				7.47	*0.008*	*-33*	*-57*	*-6*	*ERD*	*Left occipital lobe subgyral*	
				5.92	*0.047*	*-24*	*-54*	*15*	*ERD*	*Left temporal lobe subgyral*	
				6.27	0.023	54	-30	21	ERD	Right inferior parietal lobule	40
NL v baseline	0.7 v –0.5	2 v 1	15-25	7.34	0.012	-30	-75	-15	ERD	Left cerebellum posterior declive	
				6.96	0.020	-51	-21	24	ERD	Left parietal postcentral gyrus	
				6.08	0.039	30	-60	54	ERD	Right superior parietal lobe	
				6.03	0.039	42	-54	6	ERD	Right middle temporal gyrus	
				6.02	0.039	42	-69	15	ERD	Right occipital middle temporal gyrus	
NL v baseline	0.7 v –0.5	2 v 1	20-30	8.17	0.004	9	-75	30	ERD	Right occipital lobe cuneus	
				5.41	*0.043*	*36*	*-78*	*36*	*ERD*	*Right parietal precuneus*	*19*
				5.44	0.043	-57	-24	30	ERD	Left inferior parietal lobe	40
				5.33	0.047	39	-27	-15	ERD	Right temporal lobe fusiform gyrus	20
				5.31	0.047	30	-63	57	ERD	Right superior parietal lobule	7
NL v baseline	0.7 v –0.5	2 v 1	25-35		Not sig						
NL v baseline	0.7 v –0.5	2 v 1	30-40		Not sig						

SnPM group analysis of MEG Experiment 2. Naming covertly.

Condition	Timing (sec)	Trigger	Frequency (Hz)	t-value	p-level	T/C			Power	Cortical area of activity	BA
L v NL	0.3 v 0.3	1 v 2	5-15		Not sig						
L v NL	0.3 v 0.3	1 v 2	10-20		Not sig						
L v NL	0.3 v 0.3	1 v 2	15-25		Not sig						
L v NL	0.3 v 0.3	1 v 2	20-30	6.07	0.031	5	33	-6	ERD	Right limbic lobe anterior cingulate	
				5.31	*0.031*	*-6*	*35*	*-3*	*ERD*	*Left limbic lobe anterior cingulate*	
L v NL	0.3 v 0.3	1 v 2	25-35	5.32	0.020	21	-24	48	ERD	Right frontal postcentral gyrus	4
L v NL	0.3 v 0.3	1 v 2	30-40		Not sig						
L v NL	0.7 v 0.7	1 v 2	5-15		Not sig						
L v NL	0.7 v 0.7	1 v 2	10-20		Not sig						
L v NL	0.7 v 0.7	1 v 2	15-25		Not sig						
L v NL	0.7 v 0.7	1 v 2	20-30		Not sig						
L v NL	0.7 v 0.7	1 v 2	25-35		Not sig						
L v NL	0.7 v 0.7	1 v 2	30-40		Not sig						
L v baseline	0.3 v –0.5	1 v 1	5-15	5.99	0.031	27	-42	-12	ERD	Right temporal lobe fusiform gyrus	37
L v baseline	0.3 v –0.5	1 v 1	10-20		Not sig						
L v baseline	0.3 v –0.5	1 v 1	15-25	7.79	0.004	48	-9	51	ERD	Right frontal precentral gyrus	4
				6.49	0.016	-18	-90	6	ERD	Left occipital cuneus	
				5.73	0.027	-27	15	33	ERD	Left frontal sub-gyral	
				5.41	0.043	-36	-36	63	ERD	Left parietal postcentral gyrus	2
				5.40	0.043	36	-87	15	ERD	Right middle occipital gyrus	
L v baseline	0.3 v –0.5	1 v 1	20-30	7.69	0.004	-33	-3-	6-	ERD	Left parietal postcentral gyrus	
				7.54	*0.008*	*-24*	*-21*	*60*	*ERD*	*Left frontal precentral gyrus*	
				5.85	0.023	36	3	0	ERD	Right sub-lobar insula	
				5.60	0.047	-42	-9	57	ERD	Left frontal precentral gyrus	
L v baseline	0.3 v –0.5	1 v 1	25-35	7.35	0.008	-15	-18	63	ERD	Left frontal precentral gyrus	6
				6.96	*0.016*	*-30*	*-21*	*57*	*ERD*	*Left frontal precentral gyrus*	
				6.80	*0.016*	*12*	*-24*	*66*	*ERD*	*Right frontal precentral gyrus*	
				6.09	0.027	-9	36	12	ERD	Left limbic lobe anterior cingulate	
L v baseline	0.3 v –0.5	1 v 1	30-40	6.37	0.031	12	66	15	ERD	Right superior frontal gyrus	10
NL v baseline	0.3 v –0.5	2 v 1	5-15	6.53	0.027	63	-27	33	ERD	Right inferior parietal lobule	

				5.90	0.039	-9	54	-6	ERD	Left medial frontal gyrus	
NL v baseline	0.3 v –0.5	2 v 1	10-20		Not sig						
NL v baseline	0.3 v –0.5	2 v 1	15-25	6.61	0.016	-6	6	27	ERD	Left limbic cingualte gyrus	
				6.25	0.020	-12	-87	3	ERD	Left occipital lingual gyrus	17
				5.67	0.043	18	-75	30	ERD	Right occipital cuneus	7
NL v baseline	0.3 v –0.5	2 v 1	20-30	5.90	0.035	0	66	9	ERD	Left medial frontal gyrus	
NL v baseline	0.3 v –0.5	2 v 1	25-35	6.37	0.016	-33	-69	48	ERD	Left superior parietal lobule	7
				6.24	0.020	-21	-27	66	ERD	Left parietal postcentral gyrus	3
NL v baseline	0.3 v –0.5	2 v 1	30-40		Not sig						
L v baseline	0.7 v –0.5	1 v 1	5-15	5.87	0.039	33	36	-12	ERS	Right middle frontal gyrus	11
L v baseline	0.7 v –0.5	1 v 1	10-20	5.78	0.020	-39	-12	69	ERD	Left frontal precentral gyrus	6
L v baseline	0.7 v –0.5	1 v 1	15-25	7.03	0.008	-39	-15	60	ERD	Left frontal precentral gyrus	6
L v baseline	0.7 v –0.5	1 v 1	20-30	6.57	0.016	-36	-36	60	ERD	Left parietal postcentral gyrus	2
				6.57	0.016	18	-69	36	ERD	Right parietal precuneus	
				6.21	0.016	-24	-75	21	ERD	Left temporal lobe sub-gyral	
				6.12	0.031	-42	-9	54	ERD	Left frontal precentral gyrus	
				6.06	0.031	-27	-51	33	ERD	Left parietal sub-gyral	
				5.95	0.031	18	-84	21	ERD	Right occipital cuneus	18
L v baseline	0.7 v –0.5	1 v 1	25-35	6.28	0.027	-45	6	54	ERD	Left middle frontal gyrus	6
L v baseline	0.7 v –0.5	1 v 1	30-40	6.82	0.008	-30	-15	72	ERD	Left frontal precentral gyrus	6
NL v baseline	0.7 v –0.5	2 v 1	5-15	6.27	0.027	15	51	-15	ERS	Right superior frontal gyrus	
				6.26	*0.027*	*21*	*45*	*-9*	*ERS*	*Right frontal lobe sub-gyral*	
NL v baseline	0.7 v –0.5	2 v 1	10-20	6.16	0.035	-18	-78	39	ERD	Left parietal precuneus	
				5.96	0.047	-39	-12	66	ERD	Unidentified	
				5.92	*0.047*	*-42*	*-18*	*57*	*ERD*	*Left frontal precentral gyrus*	
NL v baseline	0.7 v –0.5	2 v 1	15-25	8.08	0.004	-39	-18	57	ERD	Left frontal precentral gyrus	4
				6.32	*0.027*	*-39*	*-42*	*36*	*ERD*	*Left parietal supramarginal gyrus*	*40*
				5.92	*0.035*	*-30*	*-63*	*42*	*ERD*	*Left parietal precuneus*	
NL v baseline	0.7 v –0.5	2 v 1	20-30	9.80	0.004	-30	-48	24	ERD	Left parietal sub-gyral	
				8.27	*0.008*	*-39*	*-9*	*51*	*ERD*	*Left frontal precentral gyrus*	
				8.09	*0.008*	*-24*	*-9*	*54*	*ERD*	*Left middle frontal gyrus*	
NL v baseline	0.7 v –0.5	2 v 1	25-35	5.67	0.043	-33	-57	57	ERD	Left superior parietal lobule	7
				5.63	*0.043*	*-27*	*-48*	*60*	*ERD*	*Left superior parietal lobule*	
NL v baseline	0.7 v –0.5	2 v 1	30-40		Not sig						

SnPM group analysis of MEG experiment 3. Categorising.

Condition	Timing (sec)	Trigger	Frequency (Hz)	t-value	p-level	T/C			Power	Cortical area of activity	BA
L v NL	0.3 v 0.3	1 v 2	5-15		Not sig						
L v NL	0.3 v 0.3	1 v 2	10-20	5.87	0.023	24	54	15	ERD	Right superior frontal gyrus	
L v NL	0.3 v 0.3	1 v 2	15-25		Not sig						
L v NL	0.3 v 0.3	1 v 2	20-30		Not sig						
L v NL	0.3 v 0.3	1 v 2	25-35		Not sig						
L v NL	0.3 v 0.3	1 v 2	30-40		Not sig						
L v NL	0.7 v 0.7	1 v 2	5-15		Not sig						
L v NL	0.7 v 0.7	1 v 2	10-20	4.62	0.012	-33	-36	-39	ERS	Left cerebellum posterior lobe tonsil	
L v NL	0.7 v 0.7	1 v 2	15-25		Not sig						
L v NL	0.7 v 0.7	1 v 2	20-30		Not sig						
L v NL	0.7 v 0.7	1 v 2	25-35		Not sig						
L v NL	0.7 v 0.7	1 v 2	30-40		Not sig						
L v baseline	0.3 v –0.5	1 v 1	5-15	6.54	0.012	-24	-72	54	ERD	Left parietal precuneus	7
L v baseline	0.3 v –0.5	1 v 1	10-20		Not sig						
L v baseline	0.3 v –0.5	1 v 1	15-25	8.30	0.008	12	-42	66	ERD	Right parietal postcentral gyrus	13
				7.62	*0.008*	*30*	*-69*	*48*	*ERD*	Right superior parietal lobule	
				7.95	0.008	-66	-18	27	ERD	Left parietal postcentral gyrus	
				7.91	0.008	-9	12	36	ERD	Left frontal cingulated gyrus	32
				7.22	0.012	6	-60	-15	ERD	Right cerebellum posterior declive	21
				7.04	0.012	-48	-57	24	ERD	Left middle temporal gyrus	39
				6.58	0.016	-18	-66	51	ERD	Left parietal precuneus	
				6.48	0.020	-12	-75	-6	ERD	Left occipital lingual gyrus	18
				6.38	0.023	30	24	9	ERD	Right sub-lobal extra nuclear	
				5.77	0.039	-6	-6	51	ERD	Left medial frontal gyrus	
				5,73	0.047	12	-69	48	ERD	Right parietal precuneus	
L v baseline	0.3 v –0.5	1 v 1	20-30	6.81	0.012	6	-6	39	ERD	Right limbic lobe cingulated gyrus	24
				6.75	0.012	6	21	15	ERD	Right sub-lobar extra nuclear cc	
				6.26	0.023	21	-30	72	ERD	Right parietal postcentral gyrus	3
				6.14	0.031	-9	-75	45	ERD	Left parietal precuneus	
				6.03	0.039	-39	3	51	ERD	Left middle frontal gyrus	

				5.84	0.043	39	-72	39	ERD	Right parietal precuneus	19
				5.71	0.047	-18	6	18	ERD	Left sub-lobar extra nuclear	
L v baseline	0.3 v –0.5	1 v 1	25-35	7.46	0.008	-45	51	0	ERD	Left inferior frontal gyrus	
				6.84	*0.008*	*-27*	*66*	*-9*	*ERD*	*Unidentified*	
				5.92	*0.035*	*-51*	*48*	*18*	*ERD*	*Left middle frontal gyrus*	*10*
				7.25	0.008	-30	-18	72	ERD	Left frontal precentral gyrus	
				7.00	0.008	-51	0	51	ERD	Left frontal precentral gyrus	6
				6.95	0.008	57	-15	51	ERD	Right parietal postcentral gyrus	1
				6.53	0.012	21	-30	66	ERD	Right parietal postcentral gyrus	3
				6.26	0.016	18	33	21	ERD	Right limbic anterior cingulated	32
				6.22	*0.023*	*18*	*27*	*30*	*ERD*	*Right medial frontal gyrus*	
				6.09	0.023	30	-45	0	ERD	Right sub-lobal sub-gyral	
L v baseline	0.3 v –0.5	1 v 1	30-40		Not sig						
NL v baseline	0.3 v –0.5	2 v 1	5-15	7.09	0.012	-30	-24	24	ERD	Left sub-lobar insula	
				6.10	0.023	-54	9	18	ERD	Left inferior frontal gyrus	44
NL v baseline	0.3 v –0.5	2 v 1	10-20		Not sig						
NL v baseline	0.3 v –0.5	2 v 1	15-25	7.69	0.008	63	15	6	ERD	Right frontal precentral gyrus	
				7.65	0.008	51	-18	-15	ERD	Right temporal sub-gyral	
				7.17	0.016	33	-27	57	ERD	Right frontal precentral gyrus	4
				7.10	0.020	24	-72	39	ERD	Right parietal precuneus	
				6.60	*0.023*	*21*	*-57*	*42*	*ERD*	*Right parietal precuneus*	
				6.09	*0.039*	*27*	*-78*	*27*	*ERD*	*Right occipital sub-gyral*	
				6.76	0.020	39	5	54	ERD	Right middle frontal gyrus	
				5.99	0.039	-45	-30	6	ERD	Left superior temporal gyrus	
NL v baseline	0.3 v –0.5	2 v 1	20-30	6.39	0.023	54	-15	-9	ERD	Right middle temporal gyrus	
NL v baseline	0.3 v –0.5	2 v 1	25-35	10.10	0.004	-27	-21	27	ERD	Left frontal sub-gyral	
				7.05	*0.016*	*-18*	*-6*	*-6*	*ERD*	*Left sub-lobar lentiform nucleus mgp*	
				6.80	*0.016*	*-48*	*-9*	*42*	*ERD*	*Left frontal precentral gyrus*	7
				8.22	0.004	-24	-96	9	ERD	Left middle occipital gyrus	18
				7.00	*0.016*	*-42*	*-84*	*18*	*ERD*	*Left middle occipital gyrus*	
				6.78	0.016	-48	48	0	ERD	Left inferior frontal gyrus	10
				5.89	0.035	51	-9	42	ERD	Right frontal postcentral gyrus	
				5.66	0.047	-15	-69	42	ERD	Left parietal precuneus	
NL v baseline	0.3 v –0.5	2 v 1	30-40	6.20	0.027	-39	-78	18	ERD	Left middle temporal gyrus	

L v baseline	0.7 v –0.5	1 v 1	5-15	7.11	0.020	6	66	15	ERS	Right medial frontal gyrus	10
L v baseline	0.7 v –0.5	1 v 1	10-20	6.16	0.016	-6	-60	69	ERD		
				5.77	0.023	-51	-27	63	ERD		
				5.68	0.047	-48	-21	60	ERD		
L v baseline	0.7 v –0.5	1 v 1	15-25		Not sig						
L v baseline	0.7 v –0.5	1 v 1	20-30	9.74	0.004	-48	-18	54	ERD	Left parietal psotcentral gyrus	3
				6.18	*0.016*	*-12*	*21*	*24*	*ERD*	*Left limbic lobe anterior cingulated*	
				7.13	0.008	21	-24	9	ERD	Right sub-lobar thalamus pulvinar	
				5.59	*0.023*	*27*	*-21*	*-12*	*ERD*	*Right limbic parahippocampal gyrus*	
				5.24	*0.035*	*33*	*-18*	*-30*	*ERD*	*Right limbic uncus*	
				6.16	0.020	60	-24	-30	ERD	Right frontal precentral gyrus	6
				6.15	0.020	63	-24	-30	ERD	Right inferior temporal gyrus	20
				6.09	0.020	-21	-63	51	ERD	Left superior parietal lobule	
				5.16	0.043	60	-63	15	ERD	Right occipital middle temporal gyrus	19
L v baseline	0.7 v –0.5	1 v 1	25-35	13.01	0.004	-45	-24	57	ERD	Left parietal postcentral gyrus	
L v baseline	0.7 v –0.5	1 v 1	30-40	9.45	0.004	-30	-18	48	ERD	Left frontal precentral gyrus	
NL v baseline	0.7 v –0.5	2 v 1	5-15	5.64	0.047	6	66	18	ERS	Right medial frontal gyrus	10
NL v baseline	0.7 v –0.5	2 v 1	10-20	6.75	0.012	-24	-66	-12	ERD	Left posterior cerebellum declive	
				5.37	0.043	-42	-75	30	ERD	Right temporal lobe angular gyrus	39
NL v baseline	0.7 v –0.5	2 v 1	15-25		Not sig						
NL v baseline	0.7 v –0.5	2 v 1	20-30	7.23	0.020	-42	-15	54	ERD	Left frontal psotcentral gyrus	
				7.67	0.020	36	-33	15	ERD	Right superior temporal gyrus	
				6.81	*0.020*	*36*	*-12*	*21*	*ERD*	*Right frontal sub-lobar*	*13*
				6.27	*0.031*	*57*	*-9*	*36*	*ERD*	*Right frontal precentral gyrus*	
				6.40	0.027	-60	-15	36	ERD	Left frontal precentral gyrus	4
				6.06	*0.043*	*-60*	*-15*	*27*	*ERD*	*Left parietal postcentral gyrus*	
				5.88	0.047	18	-30	69	ERD	Right frontal precentral gyrus	4
NL v baseline	0.7 v –0.5	2 v 1	25-35	9.15	0.004	-39	-24	48	ERD	Left parietal postcentral gyrus	
				6.61	*0.020*	*-39*	*-42*	*15*	*ERD*	*Left superior temporal gyrus*	
				5.74	0.047	48	-18	57	ERD	Right parietal postcentral gyrus	
				5.74	0.047	42	-24	60	ERD	Right parietal postcentral gyrus	
NL v baseline	0.7 v –0.5	2 v 1	30-40	10.92	0.004	-36	-33	39	ERD	Left inferior parietal lobe	
				7.12	*0.012*	*-51*	*-12*	*39*	*ERD*	*Left frontal precentral gyrus*	*4*
				6.90	*0.012*	*-36*	*-12*	*60*	*ERD*	*Left frontal precentral gyrus*	

				6.30	0.027	-33	-72	27	ERD	Left superior occipital gyrus	
				6.06	0.031	45	-27	54	ERD	Right parietal postcentral gyrus	
				6.04	0.031	-30	-75	42	ERD	Left parietal precuneus	19